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VOL. I.

# DIPLODOCUS (MARSH): ITS OSTEOLOGY, TAXONOMY, AND PROBABLE HABITS, WITH A RESTORATION OF THE SKELETON. 

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The bringing together of a fairly representative collection of fossil vertebrates is a work not only entailing the expenditure of considerable sums of money, but one which also calls for no little skill, energy, and ability on the part of those to whom the work is entrusted, whether they be curators, preparators, or collectors. The experienced student of vertebrate fossils alone realizes how exasperating are the many disappointments in his chosen branch of science. Many of these are unavoidable and will appear most unexpectedly even after he has been careful to eliminate those formerly due to improper field or laboratory methods by the employment of such painstaking care and improved methods of collecting and preparation as were unknown to his predecessors. Where a generation ago the extinct vertebrate life of America was but poorly represented in our museums by imperfect series of teeth and isolated bones, we are now able to study many of these extinct animals from more or less complete skeletons. For these improved conditions we are mainly indebted to the late Professor Marsh, either directly by reason of the vast collections acquired by him, or indirectly through the improved laboratory and field methods developed by him and his assistants.

It may be fairly said that there are no duplicates in any collection of vertebrate fossils, no matter how extensive such collection may be. Owing to the vicissitudes to which each skeleton was subjected immediately after the death of the animal and prior to the imbedding of the bones in the matrix, or to other vicissitudes attending
the subsequent exhumation of the remains, especially to such part of this work as has been accomplished by nature, there has resulted in the first instance, as a rule, only a partial preservation of each skeleton, and in the second, frequently the complete or partial destruction of such parts of the skeleton as were preserved in the first instance. It seldom happens that in two fossil skeletons, or even skulls, no matter how perfect they may appear, there will not be exhibited in one characters wanting in the other, due either to age, sex, or differing degrees of preservation.

Of the many exasperating disappointments just referred to, that mentioned by Professor Osborn in the second paragraph of his introduction to the description of a skeleton of Diplodocus, published as Part V., Vol. I. of the Memoirs of the American Museum of Natural History, may be cited as a common example. He says, in speaking of the discovery of the specimen, "At one time strong hopes were aroused that the entire animal would be found together. The long tail stretched off parallel with the cliff, interrupted only by a small gulley which had cut through a small section of the caudals. In front of the sacrum the dorsals stretched forward in a promising way, but the centra were wanting, and finally nothing but the neural arches remained." Strikingly similar disappointments have attended the discovery and unearthing of at least a half dozen other skeletons of Diplodocus. Happily, however, in the preserved and recovered remains of these various skeletons different parts of the frame are represented; so that by combining all, we are enabled to study the restored skeleton almost in its entirety, though still incomplete, in at least one important character, to wit, the fore feet.

The difficulties arising from the fragmentary nature of which most remains of vertebrate fossils consist when found imbedded in the rocks, are greatly increased in the Dinosauria by the enormous size attained by the individual animals in many genera. These difficulties are especially applicable to Diplodocus and the allied genera constituting the Sauropoda, which include the remains of the largest land animals known to science. These animals frequently attain to a length of over sixty feet, and there is evidence that representatives of some of the larger genera fell but little, if any, short of one hundred feet in length. Every student of the modern Cetacea is well aware of the great difficulty encountered in undertaking a comprehensive study of the osteology of that order of mammals, due chiefly to the trouble and expense incurred, on account of their size, in bringing together, preparing and caring for, sufficiently complete osteological collections. In the Dinosauria these difficulties are rendered infinitely greater, so that the task of bringing together an even fairly representative collection in any one institution, even though its resources may be considerable, is rendered exceedingly difficult, if not quite hopeless.

It is only by encouraging the collecting and investigation of the remains of these extinct and gigantic reptiles in as many institutions as possible, and by combining the results of all, that we may hope eventually to be able to trace the phylogeny of the different genera of Dinosaurs, in respect to the nature of which we are as yet quite ignorant.

The obstacles to a systematic study of the Dinosauria just enumerated serve only to increase the importance of the discovery of any additional information regarding the structure and affinities of the different genera, and to render desirable the early publication of such information. This is especially true when, as in the present case, recent discoveries have brought to light many important and hitherto unknown skeletal features and made it possible to describe, almost in its entirety, the osteology of an animal belonging to a genus, which is representative of a great and highly interesting suborder, as yet known only from fragmentary skeletons of different individuals, which for the most part pertain to different genera and species.

The material upon which the present paper is based belongs for the most part to one of two skeletons (Nos. 84 and 94). ${ }^{1}$ The former skeleton was collected by Dr. J. L. Wortman and party during the expedition of 1899 , while the latter was secured by Mr. O. A. Peterson and his assistants during the expedition of 1900, while engaged in making further excavations in the same quarry on Sheep Creek, in Albany County, Wyoming, which had yielded Dr. Wortman such excellent material during the previous season. Aside from these two skeletons of Diplodocus this quarry, or bone deposit, ${ }^{2}$ has furnished a skull and considerable portion of the skeleton of Stegosaurus as well as a great part of the skeletons of Brontosaurus and numerous remains of other Dinosaurs as yet undetermined.

For all this, and much other valuable material, brought together by the expedition of 1899 conducted by Dr. Wortman and those of 1900 carried on by Mr. Peterson under the direction of the present writer, we are indebted to the well-known generosity of Mr. Andrew Carnegie, the founder of this institution.

The work of freeing the bones from the matrix and preparing them for study has been carried on under the immediate direction of Mr. A. S. Coggeshall, chief preparator in the paleontological laboratory. In this work Mr. Coggeshall has shown exceptional skill and patience. He has been assisted by Mr. Louis S. Coggeshall and Mr. A. W. Vankirk, and in the winter months especially, by Mr. O. A. Peterson, the well-known collector as well as skilled preparator of vertebrate fossils.

[^0]The original photographs from which many of the figures have been made are by Mr. A. S. Coggeshall, while the drawings were made by Mr. Rudolph Weber and Mr. W. J. Carpenter.

The first skeleton (No. 84) has been entirely freed from the matrix and is found to consist of the right femur and pelvis complete except for the left ilium, which is for the most part wanting, right scapula and coracoid, two sternals, eighteen ribs and forty-one vertebre divided as follows : fourteen cervicals including the axis, eleven dorsals, four sacrals, and twelve caudals. These vertebre are for the most part fairly complete, though unfortunately the sacrals and anterior cervicals are more or less injured. This series of forty-one vertebre are believed to pertain to one individual and to form an unbroken series from the axis to the twelfth caudal, although as was shown in a previous paper, ${ }^{3}$ there is some evidence that there are perhaps one or more interruptions in the series and that one or more vertebre are missing. On the other hand, as will appear later, it is not eutirely impossible that at least one vertebra of this supposed series pertains to a second individual belonging perhaps to a distinct genus.

Of the second skeleton (No. 94), which pertained to a somewhat smaller individual than the first, there is a left femur, right tibia, fibula and foot, a complete pelvis, both scapulæ and coracoids, and one sternal. These remains were found associated with a few chevrons, fragments of ribs, forty-seven vertebre consisting of nine cervicals, eight dorsals, twenty caudals, and eleven other vertebree which have not as yet been sufficiently freed from the matrix to determine their characters. There were also a second pair of ischia, thus demonstrating the presence of remains of at least two individuals among these bones which were for the most part found scattered over an area about twenty feet square situated a short distance ( $8-35 \mathrm{ft}$.) south of the position occupied by the anterior cervicals of the first skeleton. (See Plate I., showing diagram of Quarry D from which the remains were taken.)

In addition to the material already mentioned reference will be made to other remains in the collection of this museum, consisting for the most part of disassociated bones, but belonging undoubtedly to Diploclocus, while for the sake of completeness in the description of the skull and dentition recourse will be had to the published memoirs of Professor Marsh and free use will be made of the excellent description by Professor Osborn of the splendid series of caudals in the collections of the American Museum of Natural History.
${ }^{3}$ Sce Science, N. S., Vol. XII., Pp. 828-830, Nov. 30, 1900.

## The Skull.

Unfortunately there is no skull of Diplodocus in our collections. ${ }^{4}$ For completeness the figures and descriptions of the skull and lower jaw of this genus given by the late Professor Marsh in his "Dinosaurs of North America" are introduced here. ${ }^{5}$ Fig. I., of the text, and Figs. 1, 2 and 3 Plate II., are after Marsh, and his description accompanying these figures is as follows:
"The skull of Diplodocus is of moderate size. The posterior region is elevated and narrow. The ficial portion is elongate and the anterior part expanded transversely. The nasal opening is at the apex of the cranium, which from this point


Fig. 1. Skull of Diplodocus longus Marsh. One-sixth natural size ; seen from below ; b, basioccipital process; eo, exoccipital ; $m$, maxillary ; $m p$, maxillary plate; o, occipital condyle ; $p$, palatine ; $p m$, premaxillary ; $p t$, pterygoid ; $p s$, parasphenoid ; $q$, quadrate ; $t$, transverse bone ; $v$, vomer. After Marsh.
slopes backward from the occiput. In front of this aperture the elongate face slopes gradually downward to the end of the muzzle, as shown in Pl. II., Fig. 1. ${ }^{6}$
"Seen from the side the skull of Diplodocus shows five openings: a small oval aperture in front, a large antorbital vacuity, the nasal aperture, the orbit, and lower temporal opening. The first of these has not been seen in any other Sauropoda, the large antorbital vacuity is characteristic of the Theropoda also, while the other three openings are present in all the known Dinosauria.
"On the median line, directly over the cerebral cavity of the brain, the type specimen of Diplodocus has also a fontanelle in the parietals. This, however, may be an individual peculiarity.
"The plane of the occiput is of moderate size, and forms an obtuse angle with the fronto-parietal surface.
${ }^{4}$ The skull of Diplodocus reported in Science, Nov. 9, 1900, p. 718, when freed from the matrix proved to belong to Stegosaurus.
${ }^{5}$ Part I., Sixteenth Annual Report, U. S. G. S., Pl. 143-244, Plates 2-85, with 66 text figures.
${ }^{6}$ References to plates and figmes are altered to agree with numbers for the same in the present paper.
"The occipital condyle is hemispherical in form, and seen from behind is slightly trilobate in outline. It is placed nearly at right angles to the long axis of the skull. It is formed almost wholly of the basioccipital, the exoccipitals entering but slightly or not at all into its composition. The basioccipital processes are large and rugose. The paroccipital processes are stout and somerwhat expanded at their extremities, for union with the quadrates.
"The parietal bones are small and composed mainly of the arched processes which join the squamosals. There is no true pineal foramen, but in the skull here figured (Plate II.) there is the small unossified tract mentioned above. In one specimen of Morosurrus a similar opening has been observed, but in other Sauropoda the parietal bones, even if thin, are complete. The suture between the parietals and frontal bones is obliterated in the present skull, and the union is firm in all the specimens observed.
"The frontal bones in Diplodocus are more expanded transversely than in the other Sauropoda. They are thin along the median portion, but quite thick over the orbits.
"The nasal bones are short and wide and the suture between them and the frontals is distinct. They form the posterior boundary of the large nasal opening, and also send forward a process to meet the ascending branch of the maxillary, thus taking part in the lateral border of the same aperture.
"The nasal opening is very large, subcordate in outline, and is partially divided in front by slender posterior processes of the premaxillaries. It is situated at the apex of the skull, between the orbits, and very near the cavity for the olfactory lobes of the brain.
"The premaxillaries are narrow below, and with the ascending processes very slender and elongate. Along the median line these processes form an obtuse ridge, and above they project into the nasal opening. Each premaxillary contains four functional teeth.
"The maxillaries are very largely developed, more so than in most other known reptiles. The dentigerous portion is very high and slopes inward. The ascending process is very long, thin, and flattened, including near its base an oval foramen, and leaving a large unossified space posteriorly. Above, it meets the masal and prefrontal bones. Along its inner border for nearly its whole length it unites with the ascending process of the premaxillary. Each maxillary contains nine teeth, all situated in the anterior part of the bone (Pl. II., Fig. 1).
"Along their upper margin, on the inner surface, the maxillaries send off a thick, ened ridge, or process, which meets its fellow, thus exeluding the premaxillaries
from the palate, as shown in Fig. 1. Above this, for a large part of their length, the ascending processes of the maxillaries underlap the ascending processes of the premaxillaries and join each other on the median line.
"The orbits are situated posteriorly in the skull, being nearly over the articulations in the lower jaw. They are of medium size, nearly circular in outline, their plane looking outward and slightly backward. No indications of the sclerotic plates have been found either in Diplodocus or in the other genera of Sauropoda.
"The supratemporal fossa is small, oval in outline, and directed upward and outward. The lateral temporal fossa is elongated, and oblique in position, bounded, both above and below, by rather slender temporal bars.
"The prefrontal and lachrymal bones are both small; the suture connecting them and also that uniting the latter with the jugal, cannot be determined with certainty.
"The postfrontals are triradiate bones. The longest and most slender branch is that descending downward and forward for connection with the jugal; the shortest is the triangular projection directed backward and fitting into a groove of the squamosal; the anterior branch, which is thickened and rugose, forms part of the orbital border above.
"The squamosal lies upon the upper border of the paroccipital process. The lower portion is thin and closely fitted over the head of the quadrate bone.
"The quadrate is elongate and slender, with its lower end projecting very much forward. In front it has a thin plate extending inward and overlapping the posterior end of the pterygoid.
"The quadratojugal is an elongate bone, firmly attached posteriorly to the quadrate by its expanded portion. In front of the quadrate it forms for a short distance a slender bar, which is the lower temporal arcade.
"The palate is very high and roof-like, and composed chiefly of the pterygoids, as shown in Fig. 1. The basipterygoid processes are elongate, much more so than in the other genera of Sauropoda.
"The pterygoids have a shallow cavity for the reception of these processes, but no distinct impression for a columella. Immediately in front of this cavity the pterygoids begin to expand, and soon form a broad, flat plate, which stands nearly vertical. Its upper border is thin, nearly straight, and extends far forward. The anterior end is acute and unites along its inferior border with the vomer. A little in front of the middle a process extends downward and outward, for union with the transverse bone. In front of this process, uniting with it and with the transverse bone, is the palatine.
"The palatine is a small semi-oval bone fitting into the concave anterior border of the pterygoid, and sending forward a slender process for union with the small palatine process of the maxillary.
"The vomer is a slender triangular bone, united in front by its base to a stout process of the maxillary, which underlaps the ascending process of the premaxillary. Along its upper and inner border it unites with the pterygoid, except at the end, where for a short distance it joins a slender process from the palatine. Its lower border is wholly free."

## The Lower Jaws.

The lower jaws are also wanting in our collections and the following brief description is taken from Marsh, as are also the figures referred to :
"The lower jaws of Diplodocus are more slender than in any of the other Sauropoda. The dentary especially lacks the massive character seen in Morosaurus, and


Fig. 2. Dentary bone of Diplodocus longus, seen from the left. One third uatural size. $a$, edentulous border ; s, symphysis. After Marsh.
is much less robust than the corresponding bone in Brontosaurus. The short dentigerous portion in front is decurved (Pl. II., Fig. 1), and its greatest depth is at the symphysis, as shown in Fig. 2. The articular, angular and surangular bones are well developed, but the coronary and splenial appear to be small."

## The Teeth.

Marsh says, "The dentition of Diplodocus is the weakest seen in any of the known Dinosauria and strongly suggests the possibility that some of the more specialized members of this great group were edentulous. The teeth are entirely confined to the front of the jaws (Pl. II., Fig. 1), and those in use were inserted in such shallow sockets that they were readily detached. Specimens in the Yale Museum show that entire series of upper and lower teeth could be separated from the bones supporting them without losing their relative position $*: *$."
"The teeth of Diplodocus are cylindrical in form and quite slender. The crowns are more or less compressed transversely and are covered with thin enamel, irregularly striated. The roots are long and slender and the pulp cavity is continued nearly or quite to the crown. In the type specimen of Diplodocus there are four teeth, the largest of the series, in each premaxillary, nine in each maxillary, and ten in each dentary of the lower jaw. There are no palatine teeth.
"The jaws contain only a single row of teeth in actual use. These are rapidly replaced, as they wear out or are lost, by a series of successional teeth more numerous than is usual in these reptiles. Fig. 3 represents a transverse section through the maxillary, just behind the fourth tooth. The latter is shown in place, and below it is a series of five immature teeth, in various stages of development, preparing to take its place. These successional teeth are lodged in a large cavity, which extends through the whole deutal portion of the maxillary. The succession is also similar in the premaxillary teeth and in those of the lower jaws."

## The Vertebre.

The skeleton of Diplodocus (No. 8t) discovered by Dr. J. L. Wortman, in 1899, has the vertebral column especially well preserved, and will be used as the basis for the following description of that part of the skeleton. In this individual alone forty-one vertebre were recovered, and they are believed to form an uninterrupted series extending from the axis to the twelfth caudal. This exceptionally well preserved series of vertebree was unearthed with great skill and care during the season of 1899 under the immediate supervision of Dr. Wortman, assisted by Messrs. W. H. Reed and A. S. Coggeshall. The locality is designated as Quarry D, and is situated about one mile south of Sheep Creek in the lower Sheep Creek Basin, in Albany


Fig. 3. Section of maxillary bone of Diplodocus longus, showing functional fourth tooth in position and five successional teeth in dental cavity; one half natural size. After Marsh. County, Wyoming. The horizon is the middle Atlantosaurus beds of Marsh (the Como stage of later authors). At this locality these beds attain a thickness of perhaps 300 feet, and are underlaid by the marine Baptonodon beds and are overlaid by the Dakota sandstones, with no apparent unconformities between the three series.

The surface in the immediate vicinity of the quarry is comparatively level, with a gentle, northerly slope. Most of the bones of the skeleton when discovered lay on
their right sides, so that this side is as a rule best preserved. The pelvis and caudal vertebre were near the surface. The caudals were interrupted at the twelfth, which lay on the line of outcrop of the bone-bearing horizon. The succeeding caudals were missing, having been removed by surface erosion. From the twelfth caudal anteriorly the vertebral column extended into the gently sloping hillside, with, however, some displacements. Unfortunately no diagram of the quarry was made, at the time of exhuming the remains, showing the relative position of each of the several vertebre and other bones as they lay imbedded in the rock. Early the following spring Mr. W. H. Reed, who assisted in taking up the skeleton, returned to the quarry and made for the writer a diagram showing the location of the various parts of the skeleton as he remembered them. This diagram has been submitted to Dr. Wortman, under whose supervision the skeleton was unearthed, and to Mr. A. S. Coggeshall, who also assisted Dr. Wortman in unearthing the remains. Both these gentlemen agree that it is essentially correct. It is reproduced in Pl. I., where it is included in the diagram of the entire quarry as worked out during the season of 1900 by Mr. O. A. Peterson and party. It occupies the central and lower portion of the plate and includes all those bones lying within the space bounded by the double full line and the broken line below, which latter marks the line of outcrop of the bone-bearing horizon in the quarry.

This diagram shows that while there were some displacements in the vertebre, these were not so great or of such a nature as to preclude the possibility of their representing in so far as they go an uninterrupted series. On the other hand the different vertebree did not lie in such relative positions as to make it certain that none were missing from the series.

Mr. A. S. Coggeshall, who assisted in unearthing the skeleton, contributes the following statement concerning its disinterment and the relative position of the different parts as they lay imbedded in the matrix. He says: "Work was carried on in both directions from the sacrum. Posteriorly the caudals extended in an almost continuous series to the twelfth, where the bone-bearing horizon emerged on the surface of the gently sloping plain. The animal had evidently fallen on his right side, and that being more deeply imbedded, was better preserved than the left. The ilia were in position, coössified with the sacrum, but the left ilium and a considerable portion of the sacral vertebree were so near the surface as to have become badly disintegrated and in a hopeless condition. In front of the sacrum, with which the last dorsal was coössified, the last seven dorsals extended in a continuous series, more or less completely interlocked by their zygapophyses. The eighth and ninth presacrals were interlocked, but shifted somewhat from their natural position, and stood on
end, the ninth lying on top of the eighth. The tenth and eleventh were also interlocked. The twelfth presacral or last (fifteenth) cervical was considerably removed from the succeeding dorsals and less so from the preceding cervicals. Commencing with the next vertebra (cervical fourteen), the direction of the entire cervical series was altered so that it lay with its axis almost at right angles to that of the dorsal series. The cervicals extended in an almost straight line from the fourteenth to the fifth, but there was a considerable gap between cervicals eleven and ten, while the axis and cervicals three, four and five were doubled back under the succeeding vertebre."
"Of the remainder of the skeleton the bones secured were found in the same relative positions as shown in the diagram (Pl. I.). Most of the ribs of the right side were not shifted far from their original position in reference to the vertebral column. The right femur was nearly in position, the left scapula and coracoid were shifted far forward from their normal position and lay parallel with the cervical series. The right pubis lay just in front of the ilium, parallel with the skeleton, with the proximal end toward the ilium, while the left pubis was found near the tenth caudal and lay at right angles to the caudal series. The ischia lay side by side, mingled with the ribs in the mid-dorsal region, while not far distant were the two sternal plates."

Throughout the excavations attending the disinterment of the above-mentioned remains strong hopes were entertained that the entire skeleton would be recovered, save only the posterior caudals, which, if ever imbedded with the other remains, had evidently been entirely removed by recent surface erosion. Late in the autumn of 1899 the work of excavating for the still missing portions was abandoned for the season. During the latter part of April and first part of May, 1900, an additional excavation was made by the present writer and a considerable area uncovered lying immediately adjacent to that worked the previous season by Dr. Wortman. This resulted in the discovery of portions of a second skeleton of Diplodocus. Early in May the work of exhuming the remains of this second skeleton was entrusted to Mr. W. H. Reed, who continued the work uninterruptedly until May 27th, when Mr. O. A. Peterson took charge, making extensive additional excavations. He continued the work throughout most of the season of 1900, assisted by Mr. C. W. Gilmore and Mr. Wm. Patton. Notwithstanding the extensive excavations made in 1900 in search of the missing portions of the skeleton discovered and taken up by Dr. Wortman during the previous season, not a single bone was found in these subsequent excavations, which can be said without doubt to pertain to that skeleton.

## General Characters of the Vertebral Column.

The Sauropoda have been considered as the least specialized of the Dinosauria, and in many respects this is doubtless true, but in its adaptation for the application of those mechanical principles which combine maximum strength with minimum weight and increased surface for muscular attachment, the vertebral column of Diplodocus exhibits a remarkable degree of specialization, unsurpassed if not unequaled by other vertebrates.

The centra throughout the entire series are invaded on either side by large lateral cavities (pleurocentral cavities), while the interior instead of consisting of solid bone is made up of numerous cavities enclosed by an intricate series of thin bony plates. These meet and cross at every conceivable angle and abut against the thin outer walls of the centra in such manner as to afford the greatest possible resistance to external strains.

The neural arches, neural spines, transverse processes, and zygapophyses are either constructed of or supported by laminæ, which come in contact with the respective parts in such manner as to give the greatest possible support with the least possible weight. The position and direction of these laminæ are so arranged in each vertebra as to afford the greatest resistance in the direction of the greatest strains and stresses which were brought to bear upon the various parts in the necessary movements during the life of the individual. By reason of this the position and direction of these laminæ are quite dissimilar in different parts of the vertebral column. Not only is any single vertebra unlike the preceding or succeeding one, but so variable are the positions of the several laminæ, buttresses, etc., that they frequently occupy quite different positions, on opposite sides of the same vertebra, sometimes resulting in a remarkable asymmetry. This asymmetry and the dissimilarity noticed in adjacent vertebre of Diplodocus render it necessary to give a detailed description of each of the presacrals even at the risk of being tedious.

Before proceeding with the detailed description of the several vertebre, it may be well to give a general description of the vertebral column as a whole.

By a glance at the accompanying restoration it will be seen that the sacrum is the central or nodal point in the vertebral column. Not only are the presacral and caudal regions subequal in length, but the individual vertebre of the former are opisthoccelous, while those of the latter are procolous. Moreover the long, coossified sacral spines are replaced anteriorly and posteriorly by the free simple spines of the adjacent dorsals and caudals, which, as we recede from the sacrum, rapidly become shorter and emarginate at the apex, resulting anteriorly in a pair of transversely placed neural spines widely separated above but converging below. These
paired spines commence with the sixth dorsal and are continued anteriorly in dorsals $5,4,3,2$ and 1 , and in most of the cervicals.

## General Description and Nomenclature of the Different Vertebral Elements.

A careful examination of any vertebra of Diplodocus, except it be a posterior caudal or anterior cervical, will show it to consist of a centrum, neural arch, neural spine, transverse processes, anterior and posterior zygapophyses, etc., or those elements usually met with in the vertebre of the reptilia and higher vertebrata. In addition to these elements, there will be seen in the vertebre of Diplodocus a number of prominent laminæ and buttresses which support the different processes and give origin to certain rather deep cavities that appear as conspicuous characters on the external surfaces of the vertebre. Owing to the extreme variation in the size, shape and position, assumed by these laminæ and cavities in the different vertebre, no little difficulty is encountered when a detailed description of the individual vertebre is undertaken. This will be facilitated by first giving a careful description of those elements as they are exhibited in that part of the vertebral column where any particular lamina or cavity is best represented, and by the employment of a precise nomenclature for each. For those elements usually found in the vertebre of all vertebrated animals, the usual and well-established nomenclature will of course be employed, while in referring to the different laminx the excellent descriptive nomenclature proposed by Osborn will be used, expanding it in one or two instances to meet the further requirements made necessary by our present more perfect material. For the different cavities a nomenclature has been devised and will be employed which it is believed is both explanatory and precise and will prove to be a useful descriptive adjunct.

The Centra.-The centra throughout the entire extent of the vertebral column have expanded extremities separated by very pronounced median constrictions, so that each centrum is in form similar to that of an hour-glass. The centra are not solid, but are composed internally of intersecting lamine arranged irregularly and abutting against and supporting the thin external walls. Externally and laterally each centrum is invaded by a pair of cavities, which may be called the pleuro-central cavities, while inferiorly there is, except in the dorsals and sacrals, a single median infracentral cavity. The centra of all the presacral vertebre are opisthocolous, while those of the postsacrals are procolous. They increase in length from the axis to the fourteenth cervical, which is the longest in the vertebral column, and then gradually decrease in length to the third dorsal. Throughout the succeeding dorsals,
sacrals, and anterior caudals they remain subequal in length, increasing somewhat in the mid-caudal region, while the posterior caudals are elongated, rod-like bones without processes.

The Neural Arches.-Throughout the entire cervical series the neural arches are low. Commencing with the anterior dorsals they increase rapidly in height and give rise superiorly to the broadly expanded diapophysial elements of the transverse processes, which appear as quite prominent features throughout the entire dorsal series.

The Neural Spines.-These are either paired, as in the cervicals and anterior dorsals, where they are placed transversely, or single, as in the posterior dorsals, sacrals and caudals. There is no nodal vertebra separating the paired from the unpaired spines, but the latter are gradually derived from the former by the convergence of the paired spines. ${ }^{7}$ This commences as a fusion in their inner and inferior margins, first noticed near the base of the spines of the second dorsal. This union becomes gradually more pronounced in the succeeding vertebre until there is formed in the minth dorsal a simple spine with emarginate extremity and finally results in the tenth and eleventh dorsals and sacrals in the production of a perfectly simple neural spine with no indication of division. The neural spines of the three true sacrals are firmly united into a single, powerful spinous process, which is the highest in the entire vertebral column. Posteriorly the division just noticed in the spines of the cervicals and anterior dorsals is partially imitated in the neural spines of the anterior caudals, but never results in anything more than an emargination of the extremities. This is most pronounced in the sixth caudal, where it attains a depth of some four or five inches. It rapidly becomes less distinct in the succeeding caudals and entirely disappears in the eleventh and posterior caudals. The sacral spines are the longest in the vertebral column. Anterior to the sacrum the spines gradually decrease in length and are directed upward and forward. Posterior to the sacrum the neural spines decrease more rapidly in length and are directed upward and backward.

The Transverse Processes. ${ }^{8}$-These are best developed on the posterior dorsals, where they spring from the point of union of the long neural spines with the neural arches, and terminate in widely expanded diapophyses. In this region the dia-

7 It is more probable that the paired spines were derived from the simple by the gradual and increased emargination of the summits of the latter. Thus the simple spines shonld be considered the primitive and the paired the specialized conditions.

8 There may be some question as to the exact homology of these processes. Osborn has referred to them both as metapophyses and as diapophyses or transverse processes. Considering their position in the anterior vertelne I hardly think they can be other than homologons with the transverse processes of mammalian osteology.
pophyses and neural spines in their relations to each other have a certain resemblance to that of the yard-arms and masts of a ship. In the seven posterior dorsals the diapophyses are situated high above the centra, all approximately in the same plane. Commencing with the fourth dorsal and continuing anteriorly the diapophyses gradually become shorter and assume a less elevated position, until in the first dorsal the position is about on a level with the superior border of the centrum. This relative position is maintained throughout the cervical series. There are prominent rugosities developed near the extremities of the diapophyses. These are smaller and look upward in the posterior dorsals, but larger, and with their surfaces directed outward in the anterior dorsals. They doubtless served for muscular attachment.

The Zygapophyses.-The caudals and posterior dorsal vertebre articulate by rather small and in the latter series much elevated zygapophyses. In the posterior dorsals the articular surfaces are small and continued into those characteristic compound articulations designated by Marsh as the diplosphenal and by Cope as the hyposphenal or hyposphenc-hypantrum articulations.

In the anterior dorsals and in the cervicals the zygapophyses are lower, more expanded transversely, with greatly enlarged articular surfaces, which describe more or less accurately the are of a circle, the anterior looking upward and inward and the posterior downward and outward.

Rib Facets.-Each dorsal vertebra in Diplodocus bears a rib, and in all but the last dorsal these ribs are movable and articulate with their respective vertebree by two facets, a tubercular facet placed on the extremities of the diapophyses and a capitular facet situated anterior and inferior to the tubercular facet and placed either on the side of the neural arch, or of the centrum. The tubercular facets in dorsals five to ten inclusive occupy the extremities of the diapophyses. They look directly outward and during the life of the individual, when in its normal quadrupedal position, these facets, together with the zygapophyses of these vertebre, lay in approximately the same plane, which was inclined slightly forward. Commencing with the fourth dorsal and in the preceding anterior dorsals the diapophyses rapidly assume a position inferior to that of the zygapophyses of their respective vertebre, and their extremities are deflected so that in the third and fourth dorsals the tubercular facets look downward and outward. In dorsals one and two this deflection becomes very pronounced, is continued as an inferior extension of the diapophyses, and the tubercular facets look directly dormward, so that in dorsal one they are on a line with the middle of the centrum.

Commencing with dorsal six and continuing throughout the succeeding dorsals the capitular facets all occupy the same plane, which is slightly inferior to that of
the tubercular facets. They are circular in outline, and occupy the extremities of short processes which spring from the sides of the anterior zygapophyses. Commencing with the fifth and continuing throughout the anterior clorsals, these facets are sessile and successively occupy less elevated positions. In the fifth dorsal the capitular facet is on the middle of the neural arch, while in dorsals four and three it has shifted down to the centrum and encroached upon the pleurocentral cavities of these vertebre. In dorsals two and one it lies wholly inferior to that cavity, and in the latter vertebre it is situated quite on the anterior and inferior margins of the centrum. In dorsals three, four, and five the capitular facet is much larger than in the preceding and succeeding dorsals, and instead of being circularisobovate in outline.

The Laminix.-These form a rather complicated system of bony plates springing from the external surfaces of the vertebre. They are quite effective as mechanical adaptations, affording greater strength and increased surface for muscular attachment with a minimum of weight. They are so arranged about the neural spines, diapophyses, transverse processes, and zygapophyses as to have afforded greatest support to those elements in those directions against which, during the life movements of the animal, there were exerted the greatest strains and stresses. The following nomenclature is in the main that of Osborn.

1. Prespinal Laminx.-Rising from the union of the prezygapophyses and extending to summit of the median or single neural spines. ${ }^{9}$
2. Postspinal Lamina.-Rising from union of postzygapophysial and extending to summit of median or single neural spines.
3. Horizontal Laminx.-Uniting the zygapophyses of opposite sides medially, and laterally connecting the prezygapophyses, diapophyses and postzygapophyses of the same side. These laminæ are divided by the diapophyses into anterior and posterior blades. These blades occupy the same horizontal plane in each of the posterior dorsals, but in the anterior dorsals and in the cervicals they are placed obliquely to the longer axis of the vertebre, and instead of occupying the same plane, they meet in the diapophyses and form a widely open letter V.
4. Prezygapophysial Lamina.-Descending from anterior border of paired spines, or diverging from same border of single spines and usually passing through anterior zygapophyses, capitular facets to superior and anterior margin of centrum. Superiorly they are usually simple, but below the zygapophyses they may be divided into two or three blades as in the anterior dorsals and most cervicals.
${ }^{9}$ This and the next lamina are not present in the paired spines. The laminæ referred to by Osborn as present on those spines are the superior blades of the pre- and postzygapophysial lamine, and not pre- and postspinal lamine.
5. Postzygapophysial Lamina.-Descending from posterior border of paired spines, or diverging from middle of single spines and passing downward through postzygapophyses to form posterior border of neural arch. Simple or branched below postzygapophyses.
6. Diapophysial Lamina.-Best shown in seventh dorsal, where it rises from the side of the simple neural spine and descends vertically through the diapophyses and continues throughout about one-half the extent of the neural arch. This lamina is divided by the diapophysis into superior and inferior blades. The superior blade is suppressed in the anterior dorsals and in the cervicals.
7. Pleurocentral Lamina.-Present only in the median and posterior cervicals and anterior dorsals, where it rises upon the anterior and superior border of the centrum, extends downward and backward, crossing and dividing into tivo parts the large pleurocentral cavities.
8. Oblique and Intersecting Laminx.-On the sides of the centra and neural arches, the latter usually supporting the zygapophyses.

The relative prominence and position of these various laminæ vary greatly in the different vertebre. They are most constant in the posterior dorsals. In these vertebre the diapophysial and horizontal lamine meet at right angles and intersect one another at a point midway between the top of the neural spine and base of centrum and midway between the anterior and posterior zygapophyses. From this point of intersection spring the tubcrcular or diapophysial rib facets. Thus the transverse processes divide the diapophysial laminæ into inferior and superior branches and the horizontal laminæ into anterior and posterior branches. The anterior branch of the latter divides in the sixth and preceding dorsals and posterior cervicals into superior and inferior blades.

## The Vertebral Cavities.

1. The Diapophysial Cavities.-The different branches of the horizontal and diapophysial laminæ radiate from the diapophyses in such manner as to form four large and subequal cavities, or pockets, left open externally. These four cavities, or pockets, are quite constant throughout the entire presacral series, and they are especially prominent in the anterior dorsals and posterior cervicals, where, from their position in regard to the diapophyses, they may be dominated respectively as the infica, supra-, post- and prediapophysial cavities. In these vertebre the diapophysial and horizontal lamine have shifted from the perpendicular and horizontal planes they occupied in the postdorsals to oblique positions.
2. The Zygapophysial Cavities.-These are four in number and in regard to the position occupied by each with reference to the zygapophyses, they may be called the supra- and infra-, post- or prezygapophysial cavities. They appear as conspicuous features on all the presacrals save the anterior cervicals, where they are less pronounced.
3. The Spinal Cavitics.-These are quite numerous and occur with more or less regularity as pockets in the surface of the single or paired spines. They are not unusually of considerable extent, as in the posterior dorsals, where they are formed and partially enclosed by the expansion of the free edges of the various laminæ that spring from the sides of such spines. Again they may be small and formed by the irregular development of secondary laminæ, or by inflections in the external walls of the spines.
4. The Pleurocentral Cavities.-These are constant throughout the entire vertebral column of Diplodocus, though varying greatly in the different regions in size, form and structure. As the name implies, they are located one on either side of each centrum, though, as frequently happens in the posterior cervicals and anterior dorsals, they may each be divided by pleuro-central laminæ into two or more partially distinct cavities. The pleuro-central cavities of opposite sides of the same vertebra are usually separated by a thin median partition, but occasionally this partition fails and they become confluent. This condition is met with more especially in the posterior cervicals.
5. The Infracentral Cavities.-Present on the inferior surface of cervicals and caudals. Absent in dorsals and sacrals.
6. The Intramural Cavitics.-Present not only within the external walls of the centra, but within those of the neural spines, transverse processes, zygapophyses, neural arches, the different laminæ, etc.; thus these elements are reduced to a complicated system of delicate intersecting laminæ which enclose the intramural cavities and abut against and give support to the external walls. They thus form a second and exceedingly efficient method of combining strength and increased surface for muscular attachment with lightness.

With this general description of the different vertebral elements we may proceed with a description of the individual vertebre.

The Cerviculs.-There are fourteen cervicals represented in our skeleton No. 84. These appear to constitute a complete series from the axis to the last cervical inclusive. The atlas would then be the only cervical vertebra missing from this series. So far as is known there is no atlas of Diplodocus in our collections. Marsh has published figures of the atlas which are reproduced here in Figs. 4 and 5. He nowhere
gives any description of this vertebra. His description of the entire vertebral column of Diplodocus in his "Dinosaurs of North America" is quite brief considering the highly interesting and remarkably specialized nature of this part of the skeleton. He dispenses with the vertebral column in two short paragraphs of eleven lines. From Marsh's figures the atlas appears to be rather short and very narrow, without expanded transverse processes. The neural spine is absent or very low, with a short anterior projection and a rather long posterior projection, with small posterior zygapophysial articular surfaces. There is a marked constriction between the neural canal and the cavity for the odontoid process. A small cervical rib is seen on the lower margin of either side of the posterior extremity.

The Axis.-The axis in this skeleton is quite complete and remarkably symmetrical for a vertebra of Diplodocus. The greatest length of the centrum is a little less


Fig. 4. Atlas of Diplodocus longus; side view; one half natural size. $a$, articular face for axis; $c$, cup ; $r$, face for rib; $z$, posterior zygapophyses. After Marsh.

Fig. 5. Atlas of Diplodocus longus; front view ; one half natural size ; c, cup ; o, cavity for odontoid process ; $l$, neural canal. After Marsh.
than the distance from its ventral surface to the top of the neural spine. Prominent postzygapophysial laminæ spring from the posterior and superior border of the neural arch. These diverge and extend upward and backward until they reach the summits of the postzygapophyses, when they are directed suddenly forwards and rapidly converge, meeting anteriorly and superiorly in the middle line to form the prespinal lamina. They thus enclose a deep postspinal cavity which opens posteriorly and externally. The anterior zygapophyses are very small and low. They occupy expansions projecting from near the middle of the sides of the neural arch, do not project forward beyond its anterior border, and look directly upward. The posterior zygapophyses are much elevated and face outward, downward and back-
ward. There are prominent rugosities just above the postzygapophyses. There is a prominent transverse process springing from the middle of the sides of the neural arch. It is broad and thin and is directed downward, backward and outward, and terminates inferiorly in a small spatulate expansion. The posterior blade of the horizontal lamina extends from the transverse process to the posterior zygapophysis at an ascending angle of $45^{\circ}$. The inferior blade of the diapophysial lamina has a horizontal position and supports the posteriorly projected transverse process by forming a short laminar buttress connecting that process with the sides of the neural arch and separating the infradiapophysial cavity from the postdiapophysial cavity. This latter cavity is separated from the supradiapophysial cavity by the posterior blade of the horizontal lamina. There is no prediapophysial cavity in the axis. A short cervical rib without anterior process springs from the side of the centrum near its inferior margin and anterior extremity. Only the base of the odontoid process is preserved, but this indicates that it was of moderate length, with a slightly concave superior surface. The centrum is strongly opisthocolous, as is the case also in all the succeeding cervicals and anterior dorsals. The central articulations of the cervicals and anterior dorsals of Diplodocus are the most finished of all the articular surfaces in the entire skeleton. There are deep pleuro-central cavities which extend anteriorly into the base of the odontoid process. Posteriorly these cavities are only separated from the cup for the ball of the succeeding vertebra by a thin plate of bone. Thus the body of the centrum is


Fig. 6. Axis of Diplodocus carnegii; seen from right side, one fifth natural size. From No. 84, Carnegie Museum collections. practically destroyed, and instead of consisting of a solid bony cylinder it is reduced to four thin plates. These unite to form the median longitudinal axis of the centrum. From this axis these plates diverge at right angles and partially enclose the neural canal and the infra- and pleuro-central cavities. At their anterior extremities they are united by a convex clisc of bone, the ball or odontoid process; while at their posterior extremities they are united by the concave disc of bone which forms the cup for the reception of the ball of the succeeding cervical. With certain variations this structure prevails throughout the centra of all the cervicals. In this manner the inferior border of the cervical centra are concave both transversely and longitudinally instead of convex transversely and concave longitudinally as in the dorsals. The principal characters of the axis are well shown in Fig. 6.

Cervicals Threc, Four, and Five.-All of these vertebre are more or less injured.

The neural spines and transverse processes especially are not well preserved. Fortunately the centra, neural arches and zygapophyses are for the most part complete. These show that commencing with the third, the anterior zygapophyses are prolonged anteriorly beyoud the ball of the centrum. There are also in each of these vertebræ, prediapophysial cavities. Owing to their imperfect condition in the region of the cervical ribs it is impossible to determine the nature of those elements in the vertebræ under consideration. In restoring these vertebre the cervical ribs have been ignored and the vertebrer restored as if they were wanting in each instance. They were undoubtedly present, but it is impossible to determine whether the transverse and capitular processes were in contact and enclosed a lateral canal and whether or not there was an anterior branch of the cervical rib. The walls of the pleuro-central cavities become successively less regular in these vertebre, and while consisting in C. 3 of a more or less flat and level floor of bone, in C. 4 and 5 the floors are invaded by several vacuities which open into intramural carities enclosed within the outer walls of the centra. Commencing with C. 3 the neural spines of these vertebree have been restored as bifid both anteriorly and posteriorly, each spine consisting of a broad thin plate of bone formed by the union of the pre- and postzygapophysial laminæ of their respective sides. These are made to appear free anteriorly and posteriorly, but united, except at their apices, throughout the inner sides; conditions which prevail in the succeeding cervicals.

Cervicals Six, Seven, Eight, Nine and Ten.-These vertebree differ so little in their more important characters that they may be very conveniently described together. They are all fairly well preserved and show certain characters which are gradually more emphasized in the succeeding vertebree of the series. Commencing with C. 6 they regularly increase in length posteriorly. The neural spines become more completely bifid, resulting in a pair of transversely placed perfectly free spines on the tenth cervical consisting of triangular plates of bone diverging superiorly and terminating at the summit in a rather blunt, rounded process. The walls of the centra in the pleurocentral cavities are successively interrupted by an increased number of vacuities and these cavities are more or less completely divided into anterior and posterior portions by strong bony plates (the pleuro-central laminæ), running from the base of the prezygapophyses obliquely downward and backward to the inferior border of each centrum. These are especially noticeable in cervicals nine and ten. Posteriorly the zygapophyses rapidly increase in size and the articular surfaces are successively more expanded, in order to gives a greater area to those surfaces of impact which were to resist the strains brought to bear upon them by the necessary movements of the neck and head during the life of the individual. As we proceed
posteriorly it will readily appear that the fulcrum formed by each anterior vertebral articulation would be subjected to successively greater strains during the process of elevation of the skull and that portion of the cervical series anterior to such vertebra. In order the better to resist these increased strains not only does the ball and socket of each vertebra successively increase in size, but the zygapophyses expand and the anterior ones, against which an increased proportion of the strain would be directed, are greatly reinfurced inferiorly by the derelopment of a second or even third inferior branch of the prezygapophysial laminæ (three in C. 10). These additional laminæ extend from the inferior surface of the broadly expanded prezygapophyses to the superior surface of the centrum, and are so arranged as to afford the greatest resistance possible to any force exerted from above. In C. 10 the median septum, which in the mid-central region in most of the cervical vertebre alone separates the pleuro-central cavities, fails, and there is in this vertebra a large vacuity


Fig. 7. Tenth, eleventh and twelfth cervicals of Diplodocus carnegii. Seen from right side; one fifteenth natural size. From No. 84, Carnegie Museum collections.
connecting these cavities. Near the lower and posterior borders of the postdiapophysial cavities there are in most of the vertebre (absent in C. 9) rather prominent foramina. In C. 10 these form a vacuity situated above the neural canal and connecting the opposite cavities. The cervical ribs are prominent, bear anterior and posterior branches, and are connected with the transverse processes thus enclosing lateral foramina. Their position throughout the entire series is inferior to the centra.

Eleventh Cervical.-This vertebra is so unlike either the immediately preceding or succeeding vertebre that if it had been found isolated it would have been unhesitatingly referred to a distinct genus. Mr. Coggeshall, however, assures me that it was interlocked with the succeeding, or twelfth cervical. The right side of this vertebra is very nearly perfect, the left was badly injured and the zygapophyses and left neural spine have been restored, not as they are shown on its right side, but as rep-
resented in the succeeding and preceding vertebrex. ${ }^{10}$ A comparison of this vertebra with C. 10 and C. 12, as shown in Pl. III. and in Figs. 7 and 8 of the text, will reveal several striking differences. The zygapophyses are short and not so extended as the extremities of the centrum. The anterior and posterior blades of the horizontal lamine are much reduced in length, and instead of uniting to form the transverse process they are widely separated and connected by a broad plate extending throughout one-half the length of the vertebra and overhanging the deep, pleuro-central cavity. The inferior blade of the diapophysial lamina is very short and extends obliquely forward and upward, meeting the descending posterior blade of the horizontal lamina at an acute angle just in front of the posterior border of the pleuro-central cavity, the two thus enclosing an exceedingly deep postdiapophysial cavity. About 65 mm . ( $2 \frac{1}{2}$ inches) in front of the junction of the horizontal and diapophysial lamine there is a large vertebrarterial canal. This opens internally into the postdiapophysial cavity and externally on the outer surface of the broad plate connecting the anterior and posterior blades of the horizontal lamina. From the position of this foramen it may possibly be homologous with the vertebrarterial canal commonly found in the cervicals of the mammalia. It is quite wanting on all the other cervicals in Diplodocus. The posterior blade of the horizontal lamina in this vertebra sends backward a rather slender process some 75 mm . (3 inches) in length, parallel with the external border of the postzygapophyses, but separated from the latter


Fig. S. Posterior view of eleventh cervical of Diplodocus carnegii (No. S4, Carnegie Museum collections), one tenth natural size. r.c., vertebrarterial canal ; v. g., groove on exterual side of postcrior zygapophyses. by a deep, narrow groove. This groove, together with the vertebrarterial canal and the long, wide, deflected plate connecting the anterior and posterior blades of the horizontal laminæ are characters entirely wanting in the other cervical vertebre of this series. The pleuro-central cavity occupies most of the side of the centrum. There is a vacuity in the mid-central region connecting the pleurocentral cavities of the opposite sides. The bottom of the pleuro-central cavity is otherwise interrupted by a complicated system of oblique and intersecting laminæ enclosing foramina leading to the intramural cavities. The infracentral cavity is very pronounced in this and the succeeding cervicals and the centra in these vertebre are

[^1]much constricted medially and expanded at their extremities. The zygapophyses are broad, with the articular surfaces transversely expanded, but contracted anteroposteriorly. The cervical rib is long and lies below the inferior border of the centrum. The combined length of the anterior and posterior costal processes are but little less than that of the centrum. The apices of the neural spines are both wanting in this vertebra. They have been restored as rather low and broad superiorly. In Fig. 7 are shown comparative views of this vertebra and cervicals 10 and 12, which immediately precede and succeed it.

The Twelfth Cervical.-This does not materially differ from the succeeding cervicals, but when seen from the side it contrasts strikingly with C. 11, as see Fig. 7, and Pl. III. There is no vertebrarterial canal. The bottom of the pleuro-central cavity is less complicated. It is invaded by four large vacuities. Three of these lie posterior and one anterior to the pleuro-central lamina, which in the vertebre of this region starts from the anterior and superior border of the pleuro-central cavity and extends downward and backward to the middle of the inferior border of the centrum, thus dividing this cavity into an anterior and a posterior moiety. The diapophysial and posterior horizontal laminæ are long, occupying about two thirds the total length of the centrum. The post-diapophysial cavity is open externally throughout its entire length in marked contrast with the condition that obtains in C. 11. There is in this vertebra a striking instance of asymmetry. 'On either side of the neural arch and directly below the postzygapophyses there is in each of the preceding and succeeding cervicals of this region a pair of large foramina about one inch in diameter placed laterally and opening into the neural canal. In C. 12 this foramen is present and of normal dimensions on the right side, but on the left instead of opening into the neural canal it terminates in a shallow pit about three fourths of an inch in depth and completely closed with bone at the bottom.

The Thirteenth Cervical.-The pleuro-central cavity is more restricted posteriorly than in the preceding cervicals. The pleuro-central lamina is especially prominent and divides this cavity into a deep, rather small anterior and a somewhat larger posterior cavity. The anterior zygapophyses are overhanging and project beyond the ball of the centrum. They are each supported inferiorly, as in the other cervicals of this region, by two prominent inferior blades of the prezygapophysial laminæ which spring from the external and superior margins of the centrum just posterior to the ball and diverge to meet the zygapophyses superiorly. A third pair of branches, the internal of the prezygapophysial as also of the postzygapophysial laminæ, converge inferiorly, meet and intersect each other just above the middle of the neural canal, where they are exceedingly thin. Below the point of intersection
they diverge again to form the superior walls of the neural canal. In this manner anteriorly the left superior border of the neural canal is formed by the inferior extension of the right prezygapophysial lamina, and the right by the left, the inferior portions of these lamine intersecting so as to form a letter X. Between the bifid neural spines there is a short spinous process homologous perhaps with the single spines of the posterior dorsals. This short median spine is present on the succeeding cervicals and anterior dorsals. Its presence in these vertebre has led me to believe those laminæ defined by Osborn as the prespinal and postspinal laminæ of the bifid vertebræ to be homologous with the pre- and postzygapophysial laminæ of vertebre with only one spine, and I have therefore called them by the latter names.

The Fourteenth Cervical.-This is the largest and slightly the longest vertebra in the entire vertebral series. The median constriction of the centrum is the most marked in the vertebral column. The pleuro central cavities are deep, but entirely separated by a median septum. The anterior zygapophyses are supported inferiorly by two powerful laminæ. The postzygapophysial laminæ are large, and the prezygapophysial much reduced. Short median neural spine. Union of rib with centrum marked by suture. The transverse process is supported inferiorly and anteriorly by a prominent lamina which is directly opposed to the posterior blade of the horizontal lamina. This is the inferior of the two anterior blades of the horizontal lamina. It is present in the succeeding vertebre and successively occupies a more horizontal position, gradually approximating that of the superior blade. In the sixth dorsal these blades are quite parallel, horizontal, and but little separated, while in D. 7 and 8 they are united throughout a portion of their length, and in D. 9 the union is complete and the anterior blade of the horizontal lamina is quite simple. See Plates III. and IV.

The Fifteenth Cervical.-The centrum of this vertebra is some two inches shorter than that of the preceding. The ball is marked by a pronounced median vertical groove also seen in the anterior dorsals. The superior of the anterior blades of the horizontal lamina has its external surface somewhat expanded and rugose. It no doubt served as a support for the muscular attachment of the heavy scapular arch. The suture for the capitular attachment of the rib is well marked. There is a distinct but short median neural spine between the two paired spines. The principal characters of the cervical vertebree are well shown in Plates III., IV., V.

## The Dorsal Vertebra.

The dorsals are distinguished from the cervicals by supporting free instead of fixed ribs and in having the inferior surface of the centra regularly convex trans-
versely instead of concave in either direction as in the cervicals. Aside from these there are no sudden changes in the transition from cervicals to dorsals. The spines continue paired, the zygapophyses broadly expanded, while the centra are long in the anterior dorsals but rapidly shorten posteriorly. All the vertebre between the last cervical and first sacral bear ribs, so that there are no lumbars in Diplodocus.

The First and Second Dorsals.-The superior branches of the anterior blades of the horizontal laminæ in these vertebræ are considerably modified in order to give a more substantial support for the suspension of the scapulæ. They are broadly expanded and inflected externally so as to present a broad, rugose external surface, much more continuous and prominent than that just described as obtaining in C. 15. The prezygapophyses in these vertebree differ from those in the former by being supported inferiorly by a pair of intersecting laminx. The paired spines are not so broad and are more acutely terminated than in the cervicals, and there is a short median spine. The pleuro-central cavities are deep and are not divided into two by the pleuro-central lamine mentioned as present in the immediately preceding cervicals. The inferior blade of the diapophysial lamina is obliquely directed downward and backward, and opposes the modified superior brauch of the anterior blade of the horizontal lamina, while the posterior blade of the latter is directly opposed to the inferior branch of its anterior blade. In this manner all these laminæ occupy oblique positions, but meet at right angles and enclose the pre-, post-, supra-, and infradiapophysial cavities. The latter in these vertebre occupy their normal positions, which has suggested the names applied to them in this paper. The extremities of the transverse processes are continued into downwardly extended diapophyses terminating inferiorly in the tubercular rib facets. The capitular facets are small prominences seen on the anterior, inferior and external margins of the centra just behind the ball and below the anterior borders of the pleuro-central carities. The two lateral laminæ projecting inferiorly and externally from the posterior portions of the cervical centra are wanting in these and the succeeding dorsals, and the inferior surface of that portion of the centra in these vertebree is uniformly convex, there being no infracentral cavity. The superior arms of the X formed by the intersection of the inner of the inferior blades of the pre- and postzygapophysial lamime are much longer than the inferior arms. The pleuro-central cavity in D. 2 is the smallest of any in the presacral series in proportion to the size of the centrum. These increase in size both anteriorly and posteriorly from D. 2. There is an elongated pit placed vertically on the apices of the balls of these centra. The centra of these vertebre rapidly become shorter, as will be seen by a refer-
ence to the measurements. The prezygapophyses extend beyond the anterior ends of the centra, while the posterior zygapophyses do not extend beyond the centra. See Plates VI. and VII.

The Third Dorsal.-Paired spines broad at base, but with pointed and widely separated extremities presenting elongated external rugosities. These spines, as those of the preceding dorsals and cervicals, are formed by the union of the superior blades of the post- and prezygapophysial laminæ. The latter in this vertebra function as the superior blades of the diapophysial lamine, which are rudimentary in D. 4 and obsolete in D. 3. The post- and prezygapophyses are much elevated, as are also the transverse processes. The superior surfaces of these processes are almost on a line with the zygapophyses. Thus the anterior and posterior blades of the horizontal lamine in this and the succeeding dorsals occupy approximately the same plane. There commences in this vertebra an approximation to the diplosphenal articulations which obtain in the posterior dorsals. The support for the postzygapophyses inferiorly is much modified. The inferior blades of the postzygapophysial lamine instead of converging and intersecting, as in the succeeding vertebre, are each divided into two branches, one vertical, the other horizontal. The former descend directly from the inner sides of the zygapophyses in sharp parallel laminæ to the outer walls of the neural canal; the latter converge and meet in the middle line a little below the zygapophyses, and form a long, very delicate, single median lamina, which descends, parallel to and midway between the vertical branches, to the superior border of the neural canal, where it again divides and sends off right and left lamine to meet the inferior extremities of the vertical blades and form the superior border of the neural canal. In this manner these laminæ enclose and bisect longitudinally an oblong with concave extremities, thus I , as shown in Pl. IV., Fig. 3. The transverse processes are widely expanded, with their extremities turned downward and backward and presenting two rugosities. The one larger and superior and external is evidently for muscular attachment. The other smaller and inferior and external is the capitular rib facet, and looks downward, outward and backward, instead of directly downward as in Ds. 1 and 2. The inferior blade of the diapophysial lamina is more perpendicular than in the preceding vertebre, but is still quite oblique. The inferior branch of the anterior blade of the horizontal lamina is still widely separated from the superior branch. The anterior zygapophyses are supported inferiorly by very powerful laminæ, but the inferior blades of the secondary intersecting lamina are wanting. The pleuro-central cavity is deep and is invaded by the capitular facet, which is supported inferiorly by a short pleuro-central lamina which bisects the pleuro-central cavity. Centrum strongly opisthoccelous. The external wall is
broken away over a portion of the posterior end of the centrum, revealing the intramural laminæ. See Pl. VI., and Fig. 3, Pl. IV.

The Fourth Dorsal.-Centrum short, with strongly convex anterior and shallow concave posterior extremity. The latter is broadly expanded transversely and vertically. Laterally and inferiorly there is a deep median constriction extending into the pleuro-central cavities. These cavities are bisected by the short pleurocentral laminæ that support the large obovate capitular rib facets, which are borne about equally by the centrum and neural arches, but extend into the pleuro-central cavities. The neural arch is elevated. The transverse processes are widely expanded, broadly rugose distally and superiorly, and bear at their extremities the tubercular facets, which look more outward and less downward and backward than in the preceding vertebre. Inferiorly the transverse process is supported by the inferior branch of the anterior blade of the horizontal lamina and by the perpendicular inferior blade of the diapophysial lamina, while on its upper side there is a rudiment of the superior blade of the latter lamina. Inferiorly the prezygapophyses are supported by a single lamina on the right side and a double one on the left. These extend from the inferior side of the zygapophyses to the superior surface of the capitular facet. The posterior zygapophyses are continued into the diplosphenal articulation so characteristic of the succeeding dorsals. These unite below to form a very sharp median lamina extending to the superior border of the neural canal. Posteriorly the transverse processes present broad, flat surfaces continuous with those of the posterior aspect of the neural arch. The extremities of the transverse processes show a rather deep posterior cavity overhung by the expanded superior rugosity. The paired spines are confluent for some distance above the superior surface of the posterior zygapophyses. They are styliform and present at their extremities rather elongated and expanded external rugosities. The median spine is less pronounced than in the preceding vertebra.

The Fifth Dorsal.-Centrum opisthocoelous, extremities widely expanded, deep median constriction, a low median ventral keel, pleuro-central cavities deep, only separated by a thin median lamina. Capitular facets obovate, very large, and borne on sides of neural arch. Neural arch much extended vertically. Zygapophyses not so broad as in preceding vertebre, continued into the characteristic diplosphenal articulations, which are supported below by a thin median lamina posteriorly, and anteriorly by a much stronger but shorter lamina parallel with that which supports the prezygapophyses and like it confluent with the capitular facet. Widely extended and stout transverse processes, with broad, distal, superior rugosities, bearing at their extremities the rather large triangular tubercular rib facets. The latter are sup-
ported inferiorly and superiorly by the diapophysial lamine which present posteriorly broad, flat and thin plates. Anteriorly and posteriorly the trimsverse process is supported by the horizontal lamina which in front has two branches. The bifid spines are confluent throughout one third their length. They are supported posteriorly by the postzygapophysial laminæ, and anteriorly by the prezygapophysial laminæ, which at the base of the spiue are suddenly deflected and merged with the diapophysial laminæ. Median spine low, with distinct pre- and postspinal laminæ.

The Sixth Dorsal.-This differs from the preceding vertebre in the more elevated and less expanded neural arch, in the bifid spines, which are confluent throughout two thirds their length, and in the more elevated position of the capitular rib facets. The emargination of the neural spines in this vertebra is 115 mm ., or $4 \frac{1}{2}$ inches. For successive emargination of spines in dorsals compare figs. in Plate VII.

The Seventh, Eighth, Niuth and Tenth Dorsals.-The centra in these vertebree are short, slightly opisthoccelous, with extremities expanded successively less constricted medially. Pleuro-central cavities, large and subequal, extending into base of neural arches. Neural arches much restricted laterally and antero-posteriorly, not wider than middle of centra. Capitular facets round and pedunculate, anterior and inferior to the small, circular, subequal, tubercular facets. The latter are borne at the extremities of the transverse processes which are more slender and somewhat less expanded than are those of the anterior dorsals, zygapophyses produced into the diplosphenal articulations. The postzygapophyses are each supported inferiorly by a narrow median lamina and by two diverging oblique lamine. Anterior zygapophyses supported inferiorly by prezygapophysial laminae and a very strong oblique lamina on sides of neural arches, which also give support to the capitular facets. Neural spines simple, but emarginate in 7,8 and 9 ; entirely simple in 10 . Strong post- and prespinal laminæ; from the external sides and near the bases of these spring the post- and prezygapophysial laminæ. Neural spines much expanded transversely by the expansion of the diapophysial laminr, which superiorly are expanded into rather broad plates presenting extensive vertical external rugosities enclosing rather deep posterior and more shallow anterior spinous cavities. The former extend throughout the entire length of the neural spines. Horizontal lamine with anterior blades bifid throughout half their length in dorsal seven, slightly bifid anteriorly in eight, and quite simple in nine and ten. See Plate VI.

The Eleventh Dorsal.-This, the last in the dorsal series, is greatly modified and functions as a sacral. It is coössified by the centrum with the true sacrals, but supports a free spine. There is no true sacral rib. The transverse process is rugose superiorly and is greatly expanded laterally and inferiorly into a broad, thin, dia-
pophysial lamina which abuts against and gives support to the anterior end of the ilium and sends off a rather delicate inferior branch which comes in contact with the lower border of the anterior blade of the ilium at its junction with the pubic peduncle. There is a large foramen between these two branches of the inferior diapophysial lamina and another and larger between the diapophyses and the inferior margin of the diapophysial lamina. There is a third and smaller foramen in the diapophysial lamina near its union with the neural arch. In addition to these foramina the cavity enclosed between the diapophysial lamine of this and the first sacral is left widely open both superiorly and inferiorly. The centrum is broad and


Fıg. 9. Inferior view of sacrum and ilia of Diplodocus carnegii (No. 94), one tenth natural size ; pb, pubic peduncle ; is, ischiac peduncle ; $a$, anterior end; $p$, posterior end.
short with pleuro-central cavity simple and of moderate depth. The zygapophyses are small and short. The articular surfaces are less extended than in any of the preceding dorsals. The neural spine is simple, very strong, and transversely expanded and rugose at the summit. There are exceedingly strong and rugose prespinal and postspinal laminæ. The superior blades of the diapophysial laminæ are well developed and have prominent superior rugosities. There was a small ossicle found between the spine of this vertebra and that of the first sacral. It is shown in position in the restoration.

The Sucrals.-The sacrum in Diplodocus may be regarded as composed of either
three, four, or five vertebree according to the individual conception as to which should be considered as sacral vertebre. If the sacrals are made to include all those vertebree that, though formerly belonging to the posterior dorsals or anterior caudals, have laterally become so modified as to function as sacrals by affording support to the ilia either by bearing true sacral ribs or by means of greatly expanded transverse processes, or by both these methods, then the sacrum of Diplodocus must be considered as composed of five vertebre. These are usually firmly coössified by their centra, though the centra of the posterior and anterior of these five vertebre may occasionally remain free or only slightly coössified. The remaining three median vertebree are always coössified by their centra and usually have their neural spines coalesced into one powerful spine, subequally expanded transversely and antero-posteriorly. These three median vertebre constitute the sacrum of Diplodocus as understood and interpreted by the late Professor Marsh, who has described the sacrum as consisting of three vertebre. Osborn, on the other hand, has included among the sacrals the posterior of the five modified vertebre, while excluding the anterior chiefly because of the absence in it of a true sacral rib springing from the body of the centrum which he finds present on all the four succeeding sacral vertebre. He therefore considers the sacrum of Diplodocus as consisting of four vertebre, the three anterior of which he considers as having constituted the primitive Dinosaur sacrum, while the fourth has been added posteriorly by the modification of the anterior caudal. The two splendid sacra belonging with skeletons 84 and 94 in our collections are unusually complete and throw much light upon the structure and development of this element in Dinosaurs. In each instance the vertebree are all firmly coössified with and give support to the ilia. In 84 the right ilium alone is preserved, and this is united to all five of the vertebree which function as sacrals either by the means of true sacral ribs or the expanded diapophysial laminae or by both these elements. All are coïssified by their centra, and the three median have their neural spines coalesced. Thus in this skeleton it will be seen that the conditions found to obtain in the sacral region are very similar to those described by Osborn except that there is a rather greater modification of the last dorsal in the direction of that which obtains in the true sacrals than was noticed by the latter in his description. (Compare the description and figures given above with those of Osborn.) In skeleton 94, however, there are noticeable certain other more marked differences, which are worthy of especial notice as bearing directly upon the nature of the primitive Dinosaurian sacrum. In this skeleton the sacrum is present, with both ilia in position. The centra of the true sacrals are all coössified as in other sacrum. The neural spines of sacrals one and two coalesce and are co-
ossified throughout their entire length as in 84, but the spine of sacral three is quite free from, though closely applied inferiorly to, that of the second sacral. This would seem to indicate that the primitive Dinosaurian sacrum consisted of two rather than three vertebre, a condition similar to that found in the Crocodilia and most other living Reptilia. The fourth sacral in No. 94 bears a free spine and is coössified by its centrum with the third and does not differ in any essential respect from that described by Osborn or from that which has been found to obtain in No. 84 of our collections. From the characters noticed above we may draw the following conclusions.

First.-That the primitive Dinosaurian sacrum consisted of not more than two vertebræ.
Second.-That in Diplodocus this primitive number of sacrals has been increased to four by the successive modification of anterior caudals resulting in the presence of three true sacrals with usually anchylosed spines and a fourth less completely modified sacrocaudal supporting a perfectly free neural spine.
Third.-That anterior to the true sacrals the last dorsal has been less modified than the anterior caudals, but so changed as to function as a sacral vertebra analogous to the so-called pelvic vertebra in Struthio.
The First, Second and Third, or True Sacrals.-As has already been noticed, these have centra not only coössified with one another, but usually with those of the immediately preceding and succeeding vertebre also. The neural spines of sacrals one and two are always coalesced with each other and usually with that of the third. The centra increase in size posteriorly. Laterally they each support a pair of sacral ribs which expand and coalesce distally to form a broad, thick plate of bone coextensive with and closely applied to the acetabular portion of the ilium with which it is united by suture. This forms a considerable portion of the inner and superior portion of the acetabulum, as will be seen by a reference to Figs. 9 and 10. These vertebre are further united with the ilia through their diapophysial laminæ, the inferior blades of which are greatly expanded and unite inferiorly with the sacral ribs and externally with the plates and crests of the ilia. They thus enclose on either side two large sacral cavities which open inferiorly and superiorly. The diapophysial lamine in the sacral vertebre divide into two blades near the base of the neural spines, one anterior, the other posterior. These blades diverge in such manner that the anterior blade of any vertebra abuts against, and coalesces with, the posterior blade of the diapophysial lamina of the immediately preceding vertebra. Thus the transverse process, as well as the inferior blade of each diapophysial lamina
in the sacrals, has its origin from two instead of one vertebra as in the dorsals and cervicals. The diapophysial process supported by the first and second sacrals is much stronger than those of the succeeding sacrals. The pleuro-central cavities are rather deep and the centra are much constricted inferiorly and medially. Between the summits of the spines of the first sacral and last dorsal there is a small bone


Fig. 10. Sacrum and ilium of Diplodocus longus Marsh ; seen from below. With anterior and posterior ends of sacrum reversed. $p b$, pubic process; is, ischiac process ; ac, acetabulum ; $b, c, d$, sacral ribs ; $f, f^{\prime}$, foramina. One tenth natural size. After Marsh.
with very rugose surface. This was present in No. 84 and in the American Museum skeleton.

The Fourth Sacral.-Pleuro-central cavities not so deep and centrum less constricted inferiorly than in the three preceding true sacrals. Rather long and strong sacral ribs spring from either side of the centrum and unite by suture with the posterior blades of the ilia. They do not coalesce with the sacral ribs of the true sacrals nor do they come in contact with the neck of the ilia in such manner as to take part in forming the acetabulum. The neural spine is free and there is a broad diapophysial process formed as in the true sacrals by the union of branches from the superior blade of the diapophysial lamina of this and the preceding vertebre.

The inferior blade of the diapophysial lamina has an extensive union with the crest and posterior margin of the ilium. It encloses posteriorly a third and larger sacral cavity which, like the two enclosed by the true sacrals, is left open superiorly and inferiorly.

In Fig. 9 is shown an inferior view of the sacrum and ilia found with skeleton 94. In this skeleton all the pelvic elements are complete, including the ilia, ischia and pubes. The sacrum is also complete save the first sacral, which is represented only by the centrum and sacral ribs. These are well preserved, but the neural spine, neural arch and diapophysial laminæ of this vertebra are for the most part wanting. The pelvic vertebra is entirely missing, having evidently become detached and removed from its normal position prior to the imbedding of the bones in the matrix. The fact that this vertebra could have been detached and separated with so little injury to the adjacent pelvic bones is in itself evidence of the imperfect union between it and those bones through the medium of the centrum and of sacral ribs. A comparison of Fig. 9 with that given by Marsh of the pelvis of Diplodocus in his "Dinosaurs of North America," and reproduced here in Fig. 10, will show that while that author was right in considering three as the number of true sacrals in Diplodocus, he mistook the anterior for the posterior end of the sacrum, since our material abundantly proves that the posterior sacral is the larger and the anterior the smaller of the series, instead of vice versa as Marsh supposed. The apparent similarity in the sacral ribs of these vertebre in the two figures is due to the altered view necessitated in the adjustment of the posterior end of the sacrum to the anterior end of the ilium in the figure given by Marsh. His material having been found isolated it was quite natural for Marsh to assume that the sacral with the larger centrum was the anterior, but the reverse has proved to be the case. In Plate IX. may be seen posterior and lateral views of the pelvis of No. 84 and a side view of a pelvis of Brontosaurus for comparison.

The Caudals.-As in a previous paper, Osborn's interpretation of the sacrals will be accepted also in this paper. The number of sacrals is thus here placed at four, while the caudals begin with the first vertebra posterior to that modified as a sacral. The twelve anterior caudals are represented and for the most part are in an excellent state of preservation in No. 84, while associated with No. 94 there were found between twenty and thirty other caudals and several chevrons. These were for the most part found disarticulated, and they doubtless pertain to two or more individuals. The excellent caudal series belonging to the American Museum of Natural History furnishes much the most trustworthy evidence regarding the number, nature and structure of the caudals in Diplodocus. After a careful study of this
series Professor Osborn has estimated the number of caudals at 37. This number will more than likely be increased by future discoveries through the addition of a number of rod-like posterior caudals now known to obtain in the tails of certain other Dinosaurs. The caudal series in Diplodocus is in length about equal to that of the presacral series. The anterior caudals are short and subequal in length, while posteriorly they are somewhat more elongated. The inferior blades of the diapophysial laminæ are broadly expanded in the anterior caudals and terminate externally and superiorly in broad rugosities. These gave great surface for the attachment of the powerful dorsocaudal musculature which in life must have obtained in this region of the vertebral column and which served to facilitate both the movements of the tail and the alteration of the anterior portion of the body from the usual horizontal or quadrupedal position to the more erect bipedal or tripodal position which was perhaps less frequently assumed during the life of the individual. The centra are invaded throughout by very deep infracentral cavities, while the pleuro-central cavities are especially pronounced in the anterior caudals. All the caudal centra are somewhat procoelous in contrast with the opisthocoelous centra of the presacrals. The centra of all the caudals are constricted medially. The neural arches are low and in the anterior caudals they are invaded by a complicated system of cavities which extend down upon the superior border of the centra. Some of these cavities are continued as foramina leading to the neural canal. Such doubtless served for the transmission of nerves. Commencing with the fourth caudal the diapophysial lamine of this and the succeeding caudals are perforated by a number of vacuities. These become elliptical in caudals five to eleven and the inner portion of the inferior blades of the diapophysial lamine in these vertebree are thus reduced to a number of parallel bars, as shown in Pl. X. In all the anterior caudals except the first the broad inferior diapophysial laminæ are strongly bent forward over the very deep and broad prediapophysial cavities. The postdiapophysial cavities are usually reduced to one or two rather large foramina just behind and at the base of the diapophysial laminæ. These lead either into the neural canal or the intramural cavities of the centra or neural arches. The infradiapophysial cavities are wanting, and the supradiapophysial, though present, are much reduced in size. The horizontal lamine are short and their anterior and posterior blades unite to form the broad inferior blade of the diapophysial. The superior branch of the latter is wanting. The pre- and postspinal and the pre- and postzygapophysial laminæ are all present and well developed. The latter is continued superiorly and instead of merging with the median postspinal lamina as in the dorsals, about midway up the spine it assumes a lateral position and is continued superiorly into an extensive,
rugose, laterally expanded lamina probably homologous with the superior portion of the superior blade of the diapophysial lamina of the dorsals. The zygapophyses are small and have their anterior articular surfaces looking upward and inward, while the posterior look downward and outward. The neural spines are simple, directed upward and backward, and decrease in length rather rapidly, but gradually, as we proceed posteriorly. The anterior spines are emarginate at the summit, and this emargination is gradually accentuated, resulting in a cleft some five inches in depth at the summit of the spine of the sixth caudal. Posteriorly to the sixth this emargination becomes successively less pronounced and the spines of the tenth and succeeding caudals terminate in rounded, somewhat expanded club-like rugosities. All the caudal spines show numerous well-marked spinous cavities. In Nos. 84 and 94 of our collections the caudal spines point


Fig. 11. Coössified caudal vertebre of Diplodocus carnegii, with chevron coössified. About the 17 th and 18 th of No. 84. Seen from the right side. One tenth natural size. more decidedly backward than they are figured in Osborn's paper. Caudals two and three of No. 84 are coössified (pathologically) by their centra. In No. 94 caudals seventeen and eighteen (?) are similarly united, as shown in Fig. 11. The principal vertebral characters mentioned above are shown in Pls. III., IV., V., VI., VII., VIII., and IX., and in the various text figures.

The Chevrons.-Commencing with the second all the caudals bear intervertebral chevrons except perhaps the small posterior ones where they are probably wanting. It was in reference to the peculiar shape of the posterior chevrons that Professor Marsh proposed the name of Diplodocus (double raftered) for these animals. Marsh, however, erroneously supposed all the chevrons borne by Diplodocus to belong to this double-branched variety. We owe to Osborn the first description of the varied forms assumed by the individual chevrons throughout the different caudal regions of Diplodocus. From Cs. 2 to 6 inclusive the chevrons are nearly straight, completely surround the hrmal canal, below which the two arms are united into a long, straight and laterally compressed spine. From C. 6 to C. 11 inclusive the chevrons are less completely coalesced below the hæmal canal, and they are curved backward and resemble somewhat the blade of a sickle. Commencing with C. 13 the chevrons of this and the succeeding vertebrec assume the form described by Marsh and instead
of terminating below the hrmal canal in a single compressed spine, as in the chevrons of the anterior caudals, these spines are expanded and present anterior and posterior branches. The posterior branches are at first the longer of the two, but they soon become subequal in length. According to Osborn all the chevrons posterior to the thirteenth caudal are open above the hæmal canal. The anterior and posterior branches of the anterior branched chevrons surround a long median opening which is confluent with the hæmal canal. While in this region the inferior branches of the chevrons are coalesced at their extremities, posteriorly they are reduced to long slender rods closely applied to, but entirely separate from one another throughout their entire length. Each chevron is united more closely to the posterior of the two vertebre with which it comes in contact than with the anterior. According to Osborn the sixteenth chevron is firmly coalesced with the centra of the eighteenth caudal in the American Museum skeleton, and among the caudals found with No. 94 in our collections there is one also bearing a coössified chevron which compares well in size and form with the eighteenth in Osborn's series. This would seem to indicate that this is a constant feature. Moreover this is just that region of the caudal series which would come in contact with the ground when in life this animal assumed a tripodal position. It is to this end no doubt that the chevrons of this region have been so modified and their union with the caudals made more complete in order the better to resist the impact brought to bear at this point by the superimposed weight of the tail and body, more especially when the animal assumed a tripodal position.

The Vertebral Formula.-From the above description it will be seen that the vertebral column of Diplodocus contains about seventy vertebree. The following formula indicates the number of these belonging to the different regions as indieated by the material at present available for study, viz., cervicals 15 , dorsals 11 , sacrals 4 , caudals 35 to 40 or even more. While these figures cannot be taken as absolutely correct, they cannot be far wrong. Whatever change either in the absolute number of vertebre in any single region, or of the vertebral column as a whole, may be necessitated by the future discovery of more perfect material, we may be perfectly sure that the relative proportions of the several regions as now understood will not be materially changed. There can be wo doubt that the pre- and postsacral regions were subequal; that the centrum was the center of power and nodal point in the verebral column; that there were no true lumbars; that the dorsals were for the most part .hort and few in number, resulting in an abbreviated dorsal region; that the ccrvicals were elongated and more numerous than the dorsals, resulting in an elongated cervical region. The elongated and increased number of cervicals, shortened and reduced
number of dorsals, absence of lumbars, rigidly coössified sacrals, are all characters found to be remarkably constant in birds, more especially in Struthio and other Ratites. They are, however, doubtless adaptive rather than genetic and are certainly indicative of no very close relationship. The one represents a condition found in highly specialized sauropod Dinosaurs, the other in comparatively generalized struthious birds. The two groups may have been derived from a common ancestral stem, or the former have given origin to the latter, but the very similar vertebral characters just noticed have without doubt been independently developed in either instance. The long tail of Diplodocus is essentially reptilian and contrasts strongly with that region of the vertebral series in recent birds, and is hardly approximated even by Archropteryx among fossil birds.

The principal dimensions of the several vertebre in Diplodocus skeleton No. 84 are given in the following table: In column 1 the greatest expanse of the transverse

|  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |

processes are given, column 2 greatest length of centra, column 3 diameter of centra at posterior extremity, 4 height of neural spines above middle of inferior border of centra in presacrals and above inferior border of posterior end in presacrals.

Measurement of Ilium and Sacrum, No. 84.

| Greatest length of | .1089 mm . |  | $42 \frac{7}{8} \mathrm{in}$. |
| :---: | :---: | :---: | :---: |
| Length of five coössified centra | 765 | ، | $30 \frac{1}{16}$ " |
| Height of coalesced spine | . 1092 | ، | 43 |
| Fore and aft diameter of three coalesced spiues at the summ | 170 | ، | $6 \frac{5}{8}$ |
| Height of coalesced spines above superior acetabular border | 970 | ، | 381 " |
| Distance from top of iliac crest to extremity of pubic pedunc | 787 | ، |  |

When adjusted to each other and placed in a straight line the forty-one vertebræ belonging with skeleton 84 form a series forty-three feet in length. Of this distance the fourteen cervicals measure 21 ft .4 in., the eleven dorsals 10 ft .8 in ., the sacrals 1 ft .9 in., and the twelve caudals the remaining 9 ft .3 in . Add to this combined length of forty-three feet two feet for the skull and atlas and 23 ft . for the difference between 9 ft ., the length of the twelve anterior caudals, and 32 ft ., the total length of the caudal series as estimated by Osborn from their quite complete caudal series, and we shall have a total length of 68 ft . for the vertebral column and skull of this skeleton of Diplodocus.

## The Neural Canal.

The neural canal is exceedingly small throughout the entire vertebral column when compared with the enormous bulk of the animal. Except in the sacrals where it is considerably enlarged, it nowhere has a diameter of more than two inches, hardly greater than that of the neural canal of a modern Rhinoceros. The small neural canal, together with the small skull and very small brain cavity of the latter are indicative of an extremely primitive nervous system and show that Diplodocus was a creature of but little mental or physical activity, sluggish in its movements, and but ill adapted to successfully compete with its contemporaries in a struggle for existence amid changing environments, especially when such changes were in any manner unfavorable to its existence.

The Sternum.-Associated with skeleton No. 84 were two somewhat irregularly shaped bones closely resembling in shape and size those figured and described by Marsh as the sternals of Brontosaurus. Marsh does not describe the sternals of Diplodocus except to say that "they are large and resemble those of Brontosaurus excelsus." These bones are somewhat ovate in outline, with the narrower extremity much thickened and rugose, while at the opposite end they expand into broad, thin
plates. They are regularly but very gently concave superiorly and convex inferiorly. Contrary to Marsh I have interpreted the thick, narrow, rugose extremities of these bones as the posterior and the thin, broadly expanded extremities as the anterior. I believe these bones to have been closely applied and firmly united by cartilage throughout three fourths of their total length as indicated by the long, straight, rugose margin which extends from the thickened extremity throughout three fourths the total length of the bone and which I have interpreted as the inner margin of


Fig. 12. Superior view of pair of sternal bones of Diplodocus carnegii (No. 84). a, anterior ends ; $p$, posterior ends ; $c, c$, surface for attachment of coracoids. About one eleventh natural size. each sternal. The outer margin of each sternal is then slightly emarginate, thin and smooth, while anteriorly they are broadly pointed and rugose. Thus the sternum of Diplodocus may be considered as composed of two broad plates of bone arranged one on either side of the median line, with their longer axes parallel with the longitudinal axis of the skeleton. These bones were firmly united by cartilage throughout three fourths of their length. They are contracted and thickened posteriorly where they present a broad rugose surface for the attachment of the cartilaginous xiphisternum and sternal ribs. Anteriorly they expand into broad thin plates with rugose anterior margins by means of which they were attached to the coracoids and thus with the scapular arch possibly without the intervention of ossified clavicles or interclavicles. Taken together the sternals of Diplodocus would thus form a shallow, raft-like sternum, the individual elements of which have a certain resemblance to those found in Iguana, in which animal, however, they are separated throughout a considerable portion of their length by the interclavicle and are contracted both anteriorly and posteriorly. The comection between the ribs and sternum was chiefly posterior and not lateral as in the Ratitre, and doubtless took place through well-developed cartilaginous or imperfectly ossified sternal ribs and xiphisterni. In Fig. 12 the sternal bones are shown in their relative positions to one another as here interpreted.

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## The Clayicles.

Thus far no clavicles have been found in the Dinosauria. Since the Lacertilia are known to possess clavicles it is not unreasonable to suppose that these bones were present in at least some genera of the Dinosauria. Associated with the skeleton of No. 84 there was found a peculiar bone which from its general form and size might very well have functioned as a clavicle. This bone is 485 mm . ( $19 \frac{1}{8} \mathrm{in}$.) in length. Throughout the greater portion of its length it is almost circular in cross section and about 45 mm . in diameter. It is bifid at one extremity and slightly expanded and somewhat flattened at the other. It is strongly curved, especially toward the bifid extremity. It is asymmetrical. If this bone is not a clavicle it is difficult to assign it any other position in this skeleton. It evidently is not a rib, and from its size and shape it could very well have been a clavicle ; moreover its position in the quarry, between the sternals and coracoids, would seem to afford additional evidence for assigning it such a position in the skeleton. 'Two views of it are shown in Fig. 13, $a, b$. If a clavicle, the convex surface was evidently the external, while the strongly inflected, bifid extremity would seem to have been the inferior and the broad, spatulate extremity the


Fig. 13. Supposed clavicle of Diplodocus carnegii (No. 84) ; a, front view ; $b$, external view. A little less than one sixth natural size. superior. We must, however, await future discoveries to determine definitely the nature and position of this bone; though I am at present strongly inclined to the opinion that it was a clavicle.

## The Ribs.

The cervical and sacral ribs and the fixed ribs of the eleventh dorsal have been described in connection with their respective vertebre and need no further notice
here, except to note that the cervical ribs in Nos. 84 and 94 are much smaller in comparison with the size of the vertebræ than are those figured by Marsh in his description of $D$. longus.

The fiee or articulating ribs of the dorsal region are ten in number on either side. Of these eighteen are preserved in No. 84 and those of the right side are essentially complete, save the second, which is wanting in the right series but present in the left, though the extreme distal end and the capitulum and tuberculum are wanting.

The first rib differs from all the others in being triangular in cross section throughout its entire length, except for a short distance just beyond the union of the capitulum and tuberculum. It diminishes regularly but very gradually in size from the point of union of the capitulum and tuberculum to the distal extremity. The latter is triangular in cross section and pointed, without any indication of the distal expansion commonly seen in the first rib of the larger mammalia. The external surface of this rib is rather broad proximally and is produced posteriorly into a rather stout blade and anteriorly into a somewhat shorter projection, so that in this region a cross-section of this rib would be T-shaped with one arm more abbreviated than the other. The capitulum and tuberculum are small, subequal, and supported by peduncles of about equal length, though the tubercular process is slightly longer and stronger than the capitular.

The second rib is wanting in the right series, but is represented in the left, though lacking the extremity and the capitulum and tuberculum. The external surface is broad and rather flat throughout the entire length. The inner surface is deeply convex throughout the greater part of the length of the rib, but toward the extremity it becomes gradually flattened, resulting in a thin, flat, spatulate extremity contrasting strongly with the triangular pointed extremity of the preceding rib.

The third rib like the first is quite complete. The tuberculum and capitulum are each pedunculate, compressed and subequal in area, while their supporting processes are about equal in length. The external surface is broad proximally, somewhat contracted medially, and slightly expanded distally, where the anterior edge is produced into a sharp ridge. The inner surface is convex. In cross section it is somewhat elliptical throughout the greater portion of its length, but proximally it is 'I-shaped, with the outer surface forming the top of the 'I.

The fourth rib is complete. The head and tuberosity of this rib are the largest of any in the series. They are borme at the extremities of their respective processes, and the capitular process is somewhat longer and more slender than the tubercular. This rib is triangular in cross section proximally but much flattened distally.

The fifth rib is in general form like the fourth. It is slightly longer and the
articular surface of the capitulum and tuberculum are smaller. The latter is borne by a very short process, while the capitular process is long and slender.

The sixth rib is of about the same length, but more slender than the fifth. It is flat throughout most of its length, but triangular proximally. The tuberculum and capitulum are small and the former is sessile while the latter is pedunculate.

The seventh rib is long and narrow. It is rather stout throughout the proximal two thirds of its. length, but distally it expands into a somewhat broader but thin blade. The tuberculum is sessile and the capitulum pedunculate. They are each circular in outline.

The eighth rib is very slender. It maintains about the same dimensions throughout its entire length, though the transverse diameter decreases somewhat distally. The tuberculum is nearly sessile, while the capitulum is supported by a slender process. The articular facets are circular in outline.

The minth rib differs from the eighth chiefly in its shorter length and more slender proportions.

The tenth is the shortest of the series. It is elliptical in cross section medially and very much flattened distally. There is a deep cavity on the posterior side between the capitular and tubercular facets.

From the following measurements it will be seen that the ribs increase regularly in length from the first to the fourth, that the fourth, fifth and sixth are subequal in length, while the posterior ribs decrease rapidly in length from the seventh to the tenth, which is the shortest in the series of free ribs.

| Measurement of Ribs. |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
| Length | of first rib |  |  | $43_{16}^{\frac{3}{6}} \mathrm{in}$. |
| " | " second rib, estimated.. | . 1300 | " | $52 \frac{3}{16}$ " |
| " | " third rib. | . 1590 | ، | $63 \frac{7}{8}$ " |
| ${ }^{6}$ | " fourth rib.. | . 1710 | ، | $68 \frac{1}{2}$ 6 |
| ، | " fifth rib. | . 1727 | " | 69 " |
| ، | " sixth rib. | . 1680 | " | $67 \frac{1}{8}$ " |
| ${ }^{6}$ | " seventh rib. | . 1580 | ، | $63 \frac{1}{4}$ " |
| " | " eighth rib. | . 1330 | ، | $53 \frac{3}{8}$ " |
| " | " ninth rib.. | . 1140 | ، | 46 " |
| " | " tenth rib. | 795 | " | 321 6 |

The Coracoid and Scapula.-These are firmly coössified in Diplodocus and enter subequally into the construction of the glenoid cavity. The scapula is much the larger element of the two. Inferiorly it is broad and with a concave external surface between the superior border of the glenoid cavity and the anterior border of the widely expanded prescapula. Superiorly and posteriorly the scapula is pro-
duced into a long, narrow and thin postscapula, slightly constricted medially, but expanded distally and with the external surface transversely convex. The coracoid is short, stout, and firmly united with the scapula, the suture remaining throughout more or less distinct. In outline the coracoid is not unlike a quadrant of an ellipse, quite thin along the periphery and much thickenetl at the central angle, which is bounded by the coracoscapular suture and the inferior border of the glenoid cavity produced into the posterior border ef the coracoid, and thus forming respectively the longer and shorter radii of an ellipse. There is a large foramen in the coracoid near the coracoscapular suture and about midway between the glenoid and anterior


Fig. 14. External view of right scapula and coracoid of Diplodocus carnegii (No. 94). About one eleventh natural size.
borders. The inferior border of the coracoid is rugose, thin, and curved rather sharply inward toward the antero-external border of the sternals to which it was perhaps not directly opposed, the union having been either cartilaginous or muscular. Taken together the coracoid and scapula may be described as forming a rather broad and thin plate, much thickened about the glenoid cavity and presenting a generally convex external and concave internal surface when viewed longitudinally. It was thin at the edges but much thickened medially. See Fig. 14.


The Fore Limb and Foot-LLittle is known of the fore limbs and feet of Diplodocus. In our collection there are no bones that can positively be referred to these parts. Marsh has figured a complete set of metacarpals which he refers to Diplodocus. Through the kindness of Professor Osborn I am able to give the following brief description of the fore limbs as represented by material in the collections of the American Museum, photographs of which have been placed at my disposal. These show that the fore limbs had a length of about three fourths of that of the hind limbs. The humerus was rather slender, somewhat compressed antero-posteriorly, and with a prominent deltoid ridge. Distally the radial articulation was external and anterior to the ulnar, so that these bones were crossed superiorly as in the mammalia. The bones of the forearm were rather long and slender, but somewhat shorter than the tibia and fibula, while the metacarpals were longer than the metatarsals and according to Oshorn the carpus was of the mesaxonic pattern and digitigrade.

The Pelvis.-The pelvis of Diplorlocus is composed of ilium, ischium, and pubis. These all unite to form the acetabulum, which is left open internally. They are not coössified. The superior border or crest of the ilium is semicircular in outline, and is much thickened and rugose. Below this the ilium is quite thin, but along the inferior border it is again thickened and about the acetabulum it attains a thickness of from six to eight inches. There are anterior and posterior expansions of the iliac crest. The former of these is much the longer. Inferiorly the acetabular border of the ilium is produced into a short posterior ischiac peduncle and a very long and stout anterior pubic peduncle. The latter was almost perpendicular when the animal was in its normal quadrupedal position, but when the bipedal or tripodal position was assumed its position became more horizontal and it thus received a correspondingly increased proportion of the weight of the elevated anterior portion of the body. The pubes are broad and stout proximally and much thickened about the acetabular border. The face for articulation with the ischium is broad and triangular. Inferiorly the pubis is produced into a rather long shaft terminating in an expanded club-like tuberosity with a broad internal rugose surface for contact with the corresponding portion of the opposite pubis. The shaft is very thin and sharp along its internal margin and much thickened and rounded externally. There is a prominent rugosity on the anterior portion of the pubis just below the articular surface for the ilium. The articular surface for the ilium is concave in all our pubes. There is a very large foramen just within the ischiac border. The broadly expanded proximal ends of the pubes are concave internally and convex externally. The ischia are the smallest of the pelvic bones. They are much expanded proximally, contracted medially, and slightly expanded distally. The shaft is trihedral in cross
section. Distally the ischia meet medially in a rather extended ischiac symphysis, usually coössified. Proximally the pubic and iliac surfaces are subequal and separated by the very broad and thickened acetabular border. The ischia when adjusted to the other elements of the pelvis present a broadly rounded inferoanterior surface and a rather deep trough superiorly, the bottom of which is formed by the approximation and partial contact of their respective shafts. The principal characters of the pelvis are shown in Pl. X., Figs. 1 and 2, and in the various text figures.


The Femur:-When compared with the femur of Brontosaurus that of Diplodocus is proportionately more slender and the head is placed at right angles to the shaft of


15


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Fig. 15. Proximal end of left femur of Diplodocus carnegii (No. 94). h, head ; g.t., greater trochanter. One fifth natural size.

Fig. 16. Distal end of left femur of Diplodocus carnegii (No. 94). c. $c$. , external condyle ; i. $c$. , internal condyle. One fifth natural side.
the bone so as to occupy the same plane as the external and internal condyles of the distal end. By reason of this a femur of Diplodocus when lying on a plane surface with posterior surface down will be supported by the head and external and internal condyles, while a femur of Brontosaurus lying in the same position would have the head directed obliquely upward and free from the supporting surface. The shaft in cross section is flattened antero-posteriorly and somewhat elongated transversely, with the internal surface deeper than the external, so that the cross section is ovate in outline, tending to form distally a more or less perfect ellipse. The greater trochanter is not distinctly separated from the head and the rugose surface of the latter is continued uninterruptedly and covers the superior surface of the greater trochanter. There is a faint constriction, but no well-defined neck connecting the head with the shaft of the femur. The external and internal condyles are large and well separated by a deep intercondylar groove. The external is divided into two parts, one external and the other internal, by a deep posterior median groove which doubtless served for the transmission of a strong tendon. The third trochanter is present, but small. Internal to and directly alongside it there is a small but quite rugose flat surface for increased muscular attachment. The third trochanter in Diplodocus is not homologous with the same trochanter in mammals. It is situated on the inner and posterior margin in Diplodocus instead of on the outer as in mammals, when present. In mammals it curves forward, while in Diplodocus it is directed directly backward. Figs. 15 and 16 represent respectively the proximal and distal extremities of a femur, No. 94, of Diplodocus, while lateral and front views are given in Pl. XI., Figs. 3 and 4, and an oblique internal front view is shown in Fig. 17.


Fig. 17. Oblique internal front view of left femur of Diplodocus carnegii (No. 94), tr., third trochanter. About one eleventh natural size.


The Tibia and Fibula.-These are rather slender bones. The fibula is much the more slender and a little longer than the tibia, since it differs from the same bone in mammals by entering subequally with the tibia into the ectocondylar articulation with the femur, while inferiorly it is produced into an extended external malleolar portion which reaches well below the distal end of the tibia, abuts against the external side of the astragalus, having entirely displaced the calcaneum, and reaching almost to the proximal ends of metatarsals four and five. It is subequal in transverse diameter throughout, but expanded antero-posteriorly at the extremities, more especially at the proximal end, where it presents a flat internal surface and rather thin anterior edge which fits into the broad groove formed by the recurved cnemial


18


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Fig. 18. Proximal end of right tibia and fibula of Diplodocus curnegii (No. 94). $t$, tibia; f, fibula. One fifth natural size.

Fig. 19. Distal end of right tibia and fibula of Diplodocus carnegii (No. 94). $t$, tibia; f, fibula; $b$, surface for metatarsals I. and II. $a$, surface for contact with external side of astragalus. One fifth natural size.
crest of the tibia, while the flattened proximal surface is closely applied to that bone. A little less than half the distance from the proximal to the distal end there is on the antero-external border of this bone a rather broad rugose area for muscular attachment. Distally the fibula is produced below the end of the tibia and expands into a broad, thick external malleolus which fits into and articulates laterally with the external surface of the astragalus. The proximal end of the tibia is much expanded antero-posteriorly and less so transversely. The shaft is quite slender, but expands again distally so as to entirely cover the superior surface of the astragalus. On its internal and posterior distal extremity it sends downward an internal malleolus which is separated from the main shaft of the bone by a deep groove for the transmission of the tendons of the flexor muscles of the foot. This process articulates
with the posterior and internal surface of the astragalus. This arrangement of the articular surfaces between the tibia, fibula, and astragalus allows of considerable movement antero-posteriorly, while at the same time prohibiting almost all lateral movement. It forms an exceedingly strong ankle joint similar to that which obtains in ungulate mammals, and was especially well adapted to resist the strains to which the ankle would have been subjected in the perambulations of so massive an animal. Figs. 18 and 19 represent respectively the proximal and distal extremities of tibia and fibula of No. 94. External and front views of these bones are shown in Pl. XI., Figs. 1 and 2.


The Pes.
The Tarsus.-The osseous portion of the tarsus in Diplodocus, as in the allied genus Brontosaurus, has been reduced to an astragalus. This is a very broad bone, deep externally, but rather thin, flat, and contracted internally. Superiorly it covers the entire distal end of the tibia, with which it articulates by a continuous articular surface, which is high and slightly convex externally, but low and somewhat excavated internally, in order to accommodate the inferiorly produced internal malleolus of the tibia. The external surface is separated from the anterior by a rather pronounced ridge, but the articular surfaces of the two faces are confluent. The anterior surface of the astragalus presents a broad, smooth, regularly convex surface for articulation with the proximal ends of metatarsals I., II., III., and the inner proximal portion of metatarsal IV. The external portion of the astragalus is high and deep and presents a deeply excavated lateral surface with an expanded anterior and inferior margin developed into a long, narrow, semi-circular articular surface, which is opposed to the internal margin of the distal end of the fibula. Posteriorly the astragalus is much constricted, and consists of a comparatively narrow ridge regularly concave vertically and conrex laterally, and separating the large external lateral cavity just mentioned from a similar, but smaller, internal lateral cavity. Inferiorly the astragalus presents a broad, rugose, and regularly convex plantar surface. This in life was evidently covered with thick cartilaginous pads which were directly op-
posed to the ground when the animal stood erect. A superior view of the astragalus is shown in Fig. 20.

The Metatarsus.-As in Brontosaurus the metatarsus of Diplodocus is composed of five well-developed functional metatarsal bones. Of these I. and II. are much stronger than III., IV. and V. and formed in life the chief support to the hind limb. Metatarsals III., IV. and V. are comparatively slender, more so than are the same elements in Brontosaurus, as compare Figs. 20 and 21. The two latter were opposed to the distal end of the fibula and not to the astragalus. Metatarsal I. is the shortest and strongest of the series. It is constricted medially, expanded vertically at the proximal, and laterally at the distal extremity, as are also the other metatarsals. Metatarsal II. is considerably longer and more slender than I. Metatarsal III. is the longest in the series, though IV.


Fig. 20. Superior view of astragalus of right pes of Diplodocus carnegii (No. 94). $t$, surface for articulation with tibia; $f$, surface for articulation with fibula; $p$, posterior side. One fifth natural size. and V. are only slightly shorter. Metatarsal IV. is the more slender of the series, while $V$. is much more robust and presents a rather broad and rugose distal surface.

The Phalaniges.-These will best be described by commencing with those of the first digit and considering each serially from the first to the fifth. The first digit supports two phalanges, one, the proximal, is short, broad and deep, and supports distally a very large, long, deep, curved and compressed claw-like ungual which in life was evidently enveloped by a horny sheath, as is evidenced by the grooved and pitted external surface. The second digit supports three phalanges. The proximal is rather longer than that of digit I. and with the three dimensions subequal. It is stout, with its inner side nearly perpendicular, while externally the surface slopes downward and outward, terminating inferiorly in a rather sharp ridge. The succeeding phalanx is reduced to a rather flat wedge of bone about one inch in thickness on its internal side and reduced to a sharp thin wedge externally. It is thus introduced as a rather thin wedge between phalanges one and three. The latter is rather large and much compressed ungual, differing chiefly in its smaller size from that of digit I. Both these unguals show an extensive proximal articular surface indicative of a considerable vertical movement of these phalanges. They are also directed rather sharply outward as well as forward. The proximal phalanx of digit III. is slightly longer than broad, while its other tivo dimensions are subequal. Phalanx
two is a short wedge-shaped bone about one inch long on its internal lateral margin and ending in a sharp lateral ridge extemally. Just beneath this bone in No. 94 of our collections, and adhering to it, there was found a very small and rather flat bone which may have been either a rudiment of a third phalanx or a sesamoid. Its position would seem to indicate the latter, though quite similar rudimentary third phalanges are known to be present in the third digit of Brontosaurus. I therefore interpret it as a rudimentary ihird phalanx. There was evidently a well-developed and functional ungual, or fourth phalanx, terminating digit III., although it was not recovered. In digit IV. the phalanges are reduced to two in number. Of these the proximal is much the larger. It is rather clepressed, but laterally ex-


Fig. 21. Front view of right hind foot of Diplodocus carnegii (No. 94). astragalus.
panded distally, and supports a small, rounded, hemispherical terminal phalanx which in life was without horny covering and was probably imbedded within the integument of the skin. No phalanges were found in position with the fifth metatarsal, but as in Brontosuuras there was most likely a small, rudimentary first phalanx without nail.

From the above description and accompanying figures it will be seen that the pes of Diplodocus is semi-plantigrade and that the weight of the body was borne by the inner side of the foot, so that digits one and two became correspondingly larger, while three, four and five through disuse have become more and more atrophied. Although in Diplodocus this had not yet resulted in the total elimination of any of the digits, yet the phalanges of the fifth have already become functionally obsolete.

It is interesting to note that while in the Mammalia digit I. it is the first to become obsolete, in the Dinosauria the reduction would seem to have commenced in the pes with the fifth, while the first digit appears as functionally the most important of the series. Though there are only two phalanges supported by it these are exceptionally well developed. Commencing with digit I. the normal number of phalanges on any digit in the pes of Diplodocus is as in most birds, always one more than the number of such digit. Thus the first digit has two phalanges, digit II. has three and the third digit has four. But in digits IV. and V. the number of phalanges


Fig. 22. Front view of right hind foot of Brontosaurus excelsus Marsh (No. 89).
are reduced to two and one respectively by atrophy due to disuse. There can be little doubt that as regards the hind feet Diplodocus walked on the inner side of the feet with the large terminal claws directed very strongly outward. The above description of the pes and hind limb of Diplodocus is based upon a right femur of No. 84 and a left femur and right tibia, fibula and foot of No. 94, complete except for the ungual phalanx of digit III. and the solitary phatanx of digit V. The principal characters are well shown in Fig. 21, while Fig. 22 shows a foot of Brontosaurus for comparison.


Fig. 23. Cross sections of left femur of Diplodocus carnegii (No. 94). $\quad a, b$, near middle of shaft; $c$, near proximal end.


Internal Structure of Limb Bones.
Marsh has described the limb bones of the Sauropoda as solid and has considered this character as of subordinal value.

A careful examination of cross sections made at almost any point in any of the larger limb bones of the Sauropoda will show that they are not solid, but consist exterually of a comparatively thin portion of rather dense, hard bone, grading off quite suddenly into a cancellated structure. This becomes more openly cancellate toward the interior, and there is formed in the center of the shafts of the larger bones distinct cavities quite devoid of osseous matter. Such conditions are especially prevalent in the femora. See Fig. 23, $a, b, c$, from photographs of cross sections taken at different points of the left femur of No. 94 .

## Taxonomy.

Marsh has elevated the Dinosauria to the rank of a subclass, dividing the different genera into three orders. One of these, the Theropoda, includes all the carnivorous Dinosauria, while the herbivorous forms are placed in two orders, the Sauropoda and the Predentata.

The Sauropoda, to which Diplodocus belongs, are the least specialized of the three Dinosaurian orders. This order embraces several genera, chiefly from the Jurassic of North America, while a few forms have been described from the Jura of Europe and the Cretaceous of India, and two or three imperfectly known genera from the Cretaceous of South America have been assigned to the Sauropoda, though some of these latter forms may perhaps yet prove to belong to the Predentata rather than the Sauropoda.

Diplorlocus was the most specialized member of the Sauropoda. This specialization is seen in the elongated caudal and cervical regions and the abbreviated dorso-
lumbar region; in the exceedingly complicated structure of the individual vertebre ; in the marked reduction in the size and number of the teeth, and in the more reduced nature of digits III., IV., and V. in the pes. Thus while the Sauropoda include the more generalized of the Dinosauria, Diplodocus exhibits the greatest specialization attained by the different genera of this order in so far as the characters of the various genera are now known.

So little is known of the structure of many of the genera of Sauropodous Dinosaurs that no attempt can at present be made to trace the phylogeny of the different genera and species. Marsh has proposed six families for the Sauropoda, viz. : (1) Atlantosauridæ; (2) Diplodocidæ; (3) Morosauridæ ; (4) Pleurocoelidæ ; (5) Titanosauridæ; (6) Cardiodontidæ. The first four of these are all from the Jurassic of North America, and the second and fourth (Diplodocidæ and Pleurocælidæ) should probably be united in one family, the Diplodocidæ. The Titanosauridæ are from the Cretaceous of India and Patagonia and may eventually prove to belong in part at least to the Predentata, while the Cardiodontidæ are from the Jurassic and lower Cretaceous of Europe.

The Sauropoda attained their greatest development both as regards size and number, not only of individuals, but of genera and species as well, at about the close of the Jurassic, while with the advent of the Cretaceous they appear to have commenced to decline, entirely disappearing toward the close of that period, where they are replaced by members of the more highly specialized carnivorous Theropoda and herbivorous Predentata, the remains of which occur in great abundance in the Laramie deposits of our Western plains.

## The Species of Diplodocus.

Marsh has proposed two species of Diplodocus. One, Diplodocus longus, is the type of the genus as well. It was first described in The American Journal of Science and Arts, Vol. XVI., Nov., 1878, p. 414, and its description was based upon certain vertebre and chevrons from the mid-caudal region. The hind limb and feet described in the same publication as belonging to the same individual evidently do not pertain to Diplodocus, but to Brontosaurus, and the feet of Diplodocus are now known to be quite different from what Marsh had supposed them to be in the article above referred to. The caudal vertebre and chevrons described by Marsh should be taken as the type in Diplodocus longus of both genus and species. The deposit from which the remains were taken was a general bone deposit or quarry, and Marsh was undoubtedly led by the proximity of the limb bones and caudal vertebre described to refer them to the same individual, a very natural conclusion, but one
which later discoveries have shown to be erroneous. The material was from Cañon City, Colorado, and was collected by Dr. S. W. Williston.

A second species, based upon material collected by Professor Arthur Lạkes, at Morrison, Colorado, was described by Marsh as D. lacustris in the same journal for February, 1884, page 166. He simply characterizes it as of smaller size and with more slender jaws. It is very probable that the Sauropoda, like the Crocodilia and most other Reptilia, continued to grow throughout the entire life of the individual, and that their immense size is indicative of a very long life. It would thus appear that size alone is an exceedingly unsatisfactory character from which to describe or determine species among these animals. Moreover, we have elsewhere spoken of the remarkable asymmetry exhibited in the


Fig. 24. Cervical vertebra of Diplodocus longus Marsh. One eighth natural size. After Marsh. same vertebra and of the marked contrast in form of the adjacent vertebre in the same series, all of which characters indicate a considerable individual variation among the Diplodocidæ. Nevertbeless there are certain structural differences that hold good with little variation throughout certain parts of the vertebral column in the known skeletons of Diplodocus that may with reason be considered as of at least specific importance. Such, for instance, are the direction of the spines of the caudals, as exhibited in the American Museum specimen and figured by Osborn and reproduced here. These in the American Museum skeleton, except in the extreme posterior portion of the tail, rise almost directly upward instead of being directed regularly upward and backward as in Nos. 84 and 94 of the Carnegie Museum collections. Compare Pls. XII. and XIII. Also the great disparity in the relative size of the cervical ribs as exhibited in our skeletons (Nos. 84 and 94) and as figured by Marsh in his description of $D$. longus are certainly of specific importance, as will be shown by a comparison of Fig. 24 (after Marsh) with the cervical series shown in Pl. III. The free spine of the third sacral in No. 94 might perhaps be also considered as of specific importance, although I am inclined to believe it more probably due to the somewhat younger age of the individual as indicated by its smaller size.

In view of the above-noted differences between $D$. longus as described by Marsh and Osborn, I consider our skeletons (Nos. 84 and 94) as belonging to a distinct species for which I propose the name of Diplodocus carnegii in honor of Mr. Andrew Carnegie, the founder of this institution, and in recognition of his interest in vertebrate paleontology; which interest he has abundantly and substantially shown in providing the necessary funds for organizing and maintaining a Section of Vertebrate Paleontology in connection with this Museum. No. 84 may be taken as the type of this new species, while No. 94 should be considered as the cotype.

The principal characters of $D$. carmegii have been given in the foregoing pages. From $D$. longus it is readily distinguishable by the smaller cervical ribs and by the caudal spines which are directed much more strongly backward |than are those in the latter species.

## Restoration of the Skeleton of Diplodocus.

The present restoration is based upon a careful study of skeletons No. 84 and 94 of the Carnegie Museum collections supplemented by the material brought together by the late Professor Marsh and now in the U. S. National Museum, and by the excellent material of the American Museum of Natural History in New York. The vertebral column is for the most part taken from No. 84, which is complete from the axis to the twelfth caudal inclusive. The atlas and skull are taken from Marsh's figures, while the posterior caudals are taken for the most part from No. 94 supplemented by Professor Osborn's figures of the splendid caudal series in the collections of the American Museum. The pelvis, scapula, ribs, coracoids, and femur are from No. 84. The tibia, fibula and pes are from No. 94, which, like the American Museum specimen, represented a somewhat smaller individual than that of No. 84, as will be seen by a comparison of the different measurements. The fore limbs and feet are from a second individual in the collections of the American Museum, for the use of which I am indebted to the kindness of Professor H. F. Osborn, to whom also I wish to make acknowledgment for several valuable suggestions which have been especially helpful in the preparation of the present paper.

In the present restoration the animal is represented in a quadrupedal position as seen from the right side. The position is one which it is believed the animal must have frequently assumed when feeding upon the soft and succulent plants that grew in abundance along the shores of the shallow waters about and in which these Dinosaurs lived in late Jurassic and early Cretaceous times. The slender skull, provided with but few and rather weak teeth, was supported by a very long and flexible neck which permitted of an almost unlimited variety of movements throughout a considerable arc.

The restoration at once reveals the unusual proportions of Diplodocus. The remarkable long neek and tail contrast strikingly with the short body. The hind limbs are longer than the fore limbs, and this fact, together with the enormous elevation of the spines of the sacrals and posterior dorsals, fixes the sacral region as the highest in the vertebral column, a determination first made by Osborn. The powerful ilia, firmly united to the rigidly coössified sacrals with lofty coalesced spines, together with the other pelvic elements proportionately well developed, at once emphasizes the paramount importance of the pelvic region and fixes it as the center of power and motion. The elevated spines, long chevrons, and broadly expanded and rugose diapophyses of the anterior caudals, indicate for this region a very powerful musculature which in life enabled this appendix to serve both as an effective weapon and an important organ of locomotion both for swimming when in water and as a balancing organ when on land, while the modified nature of the chevrons of the mid-caudal region indicate the point of contact of the tail with the earth attending the different positions habitually assumed during the life of the individual. The body proper was abnormally short in comparison with the neck and tail. There were no true lumbars, all the vertebre of the dorsolumbar region having borne ribs. While the body proper was unusually short, it was deep, as indicated by the ossified ribs of the mid-dorsal region, which have a length of over five feet, while the absolute girth of the body was probably much increased by cartilaginous abdominal and sternal ribs, which latter doubtless served to attach the ossified ribs to the sternal elements. Thus, notwithstanding the extremely short nature of the body of Diplodocus, the capacity of the abdominal and thoracic cavities were rendered adequate by its great depth. Moreover, the actual length of the thoracic cavity is much increased from the scapulas being partially swung from the posterior cervical.

The fore limbs and feet of Diplodocus, and, indeed, of the Sauropoda generally, are less perfectly known than any of the other portions of the skeleton. In the present restoration they are entirely taken from materials in the collections of the American Museum of Natural History in New York. Concerning the humerus, radius and ulna, there can be no mistake, as these are drawn from photographs of actual specimens loaned by Professor Osborn for the purpose. Of the arrangement of the elements of the manus there is much less certainty. As yet no manus of Diplodocus or of the other genera of Sauropoda has been found in position. The lack of a close and exact articulation between the bones in the Sauropoda renders it impossible to place the different elements of the manus, when found separated, in their exact and proper positions with a degree of absolute confidence. Professor Osborn in his study of the limbs of Dinosaurs has considered the fore feet of the

Sauropoda as constituted on the mesaxonic plan, and in the present restoration that plan has been followed entirely upon the authority of Osborn. There is, indeed, a striking contrast between the supposed mesaxonic arrangement in the manus and the entaxonic arrangement that is known to obtain in the pes. Nevertheless Osborn has shown that there are some very strong evidences in favor of such an arrangement in the fore feet, and strikingly different as would then be the structure of the fore and hind feet, yet it would be no more striking that which is known to prevail among certain recent sloths in the Mammalia.

The most striking features brought out by the present restoration are the ridiculously short dorsolumbar region and the exceedingly small size of the skull and anterior cervicals when compared with the great length and size of the animal. The abbreviation of the dorsolumbar region is accomplished both by the reduced number of dorsals and by the shortening of the centra of the individual vertebre of this region. While in the caudal and cervical regions length is gained both by an increase in the number and in the length of the individual vertebre in either series, in the caudal series length is gained chiefly by increasing the number of vertebre, while the cervical region owes its elongation for the most part to the great length of the individual vertebre, especially in the posterior and mid-cervical regions, though the number of cervicals is also considerable, not less than fifteen.

## Probable Habits of Diplodocus.

As first noted by Professor Marsh, the position of the narial opening at the apex of the cranium in Diplodocus is indicative of aquatic habits. Moreover, the extreme modifications of the limb bones, vertebræ, and, indeed, of all the larger bones of the skeleton, whereby the greatest possible area for muscular attachment is afforded with the least possible increase in weight, are adaptations admirably calculated to increase very considerably the buoyancy of so massive an animal when in water. The deeply pitted articular surfaces of the various parts of the appendicular skeleton are perhaps indicative of thick cartilaginous pads interposed between such surfaces at the various joints of the limbs and feet. This want of closely fitting and well-defined articular surfaces would appear to afford additional evidence in favor of aquatic habits, and that the movements of the animal when on land were decidedly slow and clumsy, for had Diplodocus and its ancestors been addicted to terrestrial life the habitual support of so massive a body in so light a medium as the atmosphere would scarcely have failed to produce closely applied and well-finished articular surfaces, similar to those which obtain in such members of the Theropoda as are of undoubted terrestrial habits. From the above consideration I am inclined
toward the opinion that Diplodocus was essentially an aquatic animal, but quite capable of locomotion on land. Though living for the most part in the more important rivers and freshwater lakes, it may not infrequently have left the water and taken temporarily to the land, either in quest of food or in migration from one to another of adjacent bodies of water. Not only would an aquatic life seem to harmonize best with the anatomical characters of Diplodocus as we know them, but such a habitat would also afford these comparatively helpless animals the greatest possible protection from the huge terrestrial carnivorous Dinosaurs which lived contemporaneously with them and were undoubtedly their constant enemies.

Bearing in mind the enormous size of the animal and the great quantity of food necessary for its sustenance, in consideration with the extremely small and almost edentulous skull, it will readily appear how important to the existence of these animals was the nature of their environments. They were remarkably ill adapted for maintaining themselves amidst varying conditions. Not only was an almost inexhaustible food supply necessary to their existence, but they were also equally dependent upon the nature of the food. The small, pointed, imperfectly socketed rake-like teeth of Diplodocus, only present in the anterior portion of the mouth, were of little or no use as masticating organs, but would have served the animal very well as prehensile organs useful in detaching from the bottoms and shores the tender, succulent aquatic and semi-aquatic plants that must have grown in great abundance in the waters and along the shores of the Jurassic streams and lakes in and about which these animals lived. It is not improbable that during the period when these huge dinosaurs lived and flourished over what is now New Mexico, Colorado, Wyoming, Montana, and the Dakotas there prevailed throughout this region physical conditions somewhat similar to those which exist to-day in tropical America and more especially over the coastal plain of the lower Amazon with its numerous bayous and islands, or the more elevated valleys of the interior in the Brazilian provinces of Amazonas and Matto Grosso with their numerous lakes and large rivers surrounded by a dense tropical vegetation with broad, level valleys subject to periodical inundations. It is only in the midst of such conditions that we can suppose it was possible for these animals to have existed, while comparatively very limited climatic or other physical changes affecting either the abundance or nature of their food supply would have rendered their existence precarious and finally led to their extermination. During the late Jurassic and in early Cretaceous times the western portion of the great interior basin of North America was but slightly elevated, and for the most part consistod of vast morasses with occasional open bodies of water connected by deep but sluggish streams. Here in the midst
of an exceedingly luxuriant vegetation, in a moist tropical climate, lived Diplodocus and numerous other huge members of the Sauropoda, as well as other Dinosaurs. If we picture these or similar conditions as having prevailed over this region in middle Mesozoic times we may form a very fair idea of the probable environments attending the existence of these monsters. With the beginning of the Cretaceous there began a subsidence over this region, and a great inland sea was formed which gradually encroached upon the halitat of these animals, more and more restricting the area adapted to them, so that at about the commencement of the Upper Cretaceous the entire region formerly occupied by them had become a shallow sea save only certain islands of limited extent and perhaps otherwise poorly adapted as the homes of such animals as were the Sauropoda. In this manner was accomplished the final extermination of this group of Dinosaurs, while the carnivorous Theropoda and the herbivorous Predentata, through their greater ability to adapt themselves to the changed environments, continued on throughout the entire Cretaceous and have left their remains in great abundance imbedded in the sandstones and shales of the Laramie, the closing period of Mesozoic times.

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## Explanation of Plates.

Plate I. Diagram of quarry C, near Camp Carnegie on Sheep Creek, in Albany County, Wyoming. The bones lying within the double full line belong to Diplodocus skeleton No. 84. Those in the upper left-hand corner belong to Diplodocus skeletou No. 94 . Those to the right of skeleton 84 belong chiefly to Brontosaurus, Morosaurus, and Stegosaurus. The several parts of the various skeletons are represented in the relative position in which they were found imbedded in the matrix. The dotted line represents the line of outcrop on the hillside of the bone-bearing horizon. The irregular full line shows the limits to which the quarry was worked during the season of 1900 , by Mr. Peterson and party. The double full line shows the limits to which the quarry was worked in 1899 by Dr. Wortman and party. The caudal vertebræ of No. 84 began near the line of outcrop, while the last of the cervicals were found near the upper end of the quarry as worked out in 1899 . The scale is about 7 feet to the inch.
Plate II. Skull of Diplodocus longus Marsh, after Marsh.
Fig. 1. Side view of skull in U. S. National Museum.
Fig. 2. Front view of same skull.
Fig. 3. Top view of same skull.
All figures one sixth natural size.
Plate III. Cervical series of Diplodocus carnegii (No. 84), complete except for atlas. Seen from right side; one tenth natural size.
Plate IV. Cervical series of Diplodocus carnegii (No. 84), complete except atlas, from photographs ; one eleventh natural size. Seen from right side.

Plate V. Cervical series of Diplodocus carnegii (No. 84). Anterior view, from photographs. About one eleventh uatural size. Series complete, except atlas.
Plate VI. Cervical series of Diplodocus carnegii (No. 84). Posterior view, from photographs. About one eleventh natural size. Series complete save atlas, which is wanting.

Plate VII. Ten anterior dorsals of Diplodocus carnegii (No. 84), seen from right side, and posterior view of third dorsal. All figures one tenth natural size. al, prespinal lamina; $h l$, horizontal lamina ; $a z l$, prezygapophysial lamina; ol, oblique lamina ; $d l$, diapophysial lamina; pzl, postzygapophysial lamina; $t$, tubercular facet; $c$, capitular facet; $m s$, median spine.
Plate VIII. Ten free dorsals of Diplodocus carnegii (No. 84). From photographs about one twenty-second natural size. Columu 1, anterior view ; column 2, posterior view ; column 3 , as seen from right side. Vertebre arranged in serial order from dorsal 1 to 10 in each column, commencing at the right with No. 1 and ending on the left with 10 .

Plate IX. Twelve anterior caudals of Diplodocus carnegii (No. 84). Column 1, posterior view; column 2, anterior view; column 3, as seen from right side. Vertebræ are arranged consecutively from 1 to 12 , commencing at the right in either column. 2 and 3 are coössified and appear as one vertebra in columns 1 and 2. All figures about one twenty-second natural size.
Plate X. Comparative views of pelvis of Diplodocus and Brontosaurus.

1. Side view of pelvis of Diplodocus carnegii (No. 94). About one eleventh natural size. From a photograph. Owing to crushing, the sacral spines appear rather low, and since the anterior blade of the ilium bends strongly outward, that element is foreshortened and appears rather more pointed than it should. Seen from right side.
2. Posterior view of same specimen.
3. Sacrum and ilium of Brontosaurus seen from right side. Pubic peduncle and anterior blade of ilium are incomplete, as is also the top of sacral spines.

All figures about one eleventh natural size.
Plate XI. Hind limb and foot of Diplodocus carnegii.

1. Front view of right tibia, fibula, and foot of Diplodocus carnegii (No. 94).
2. External view of same.
3. Front view of right femur (No. 86).
4. External view of same.

All figures about one eleventh natural size.
Plate XII. Pelvis and caudal series of Diplodocus longus Marsh. Seen from left side, about one fortieth natural size. After Osborn.
Plate XIII. Restoration of Diplodocus carnegii Hatcher, one thirtieth natural size.


Diagram of Quarry C. Showing positions of Skeletons 84 and 94. Scale 7 feet to the inch.


Skull of Diplodocus Longus Marsh, after Marsh. $\frac{1}{6}$ nat. size.
Memoirs Carnegie Museum, Vol. I.



Memoirs Carnegie Museum, Vol. I.
Pl.ate IV.


Cervical Series of Diplodocus Carnegit Hatcher (No. St). Atlas wanting



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Plate X.

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[^0]:    1 The numbers in this paper refer to the Department numbers in the Card Catalogne of Vertebrate Fossils in the Carnegie Museum.
    ${ }^{2}$ Known as Quarry D on field labels and notebooks.

[^1]:    ${ }^{10}$ The work of freeing these vertebre from the matrix and restoring them was for the most part done during my absence in the field. Unfortunately no drawings or photographs were taken prior to the process of restoring with colored plaster.

[^2]:    ${ }^{11}$ Marsh places the narrow thick ends of these bones as anterior in Brontosaurus, while in Morosaurus he considers the narrow extremities as posterior. I believe the latter the correct interpretation, since it does not appear possible that the coracoids could have approached sufficiently elose to one another to have artieulated with the narrow thickened extremities which seem so well adapted for the support of the sternal ribs and xiphisterni.

